Paleodiversity of Chondrichthyan Faunas from the Neogene of Tropical America

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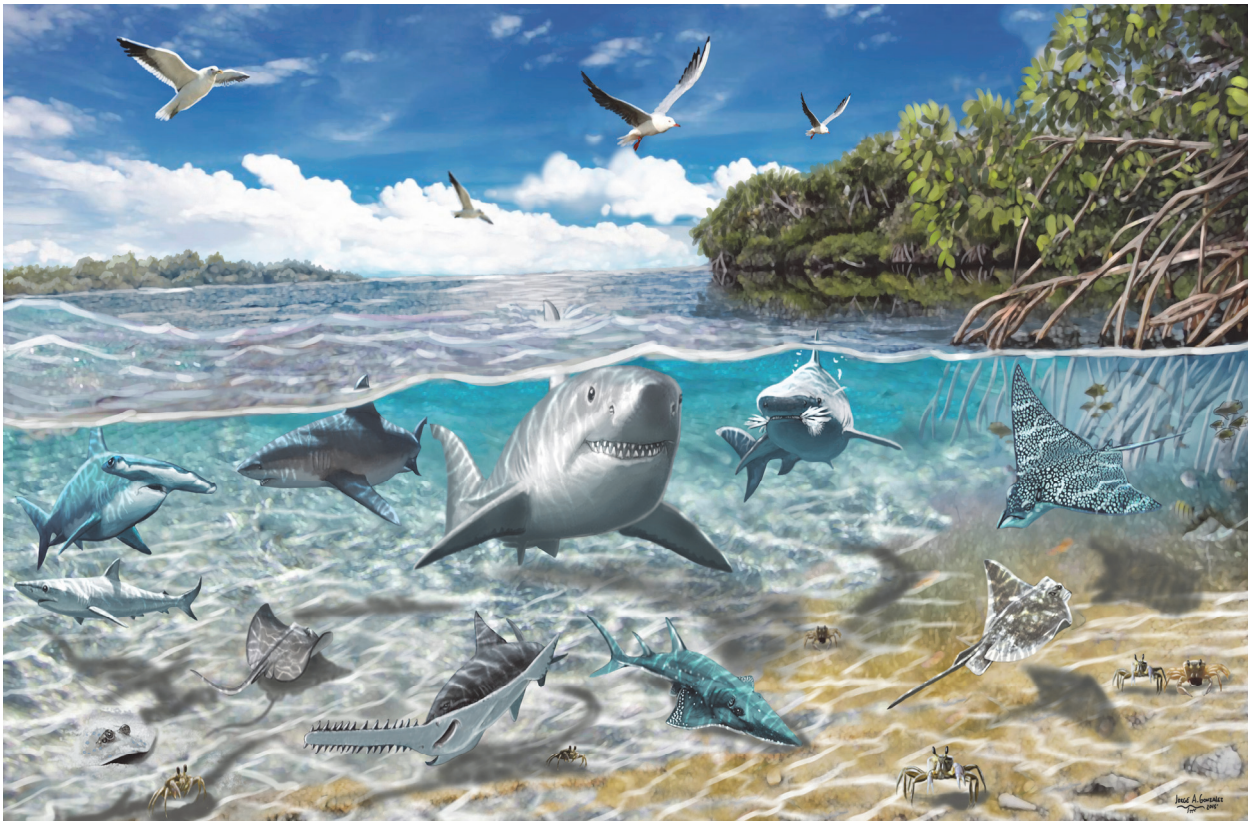
PALAEODIVERSITY OF CHONDRICHTHYAN FAUNAS FROM THE NEOGENE OF TROPICAL AMERICA



Jorge Domingo Carrillo Briceño

Universität Zürich, 2016

Title page image:

Restoration of diverse sharks and rays in coastal lagoon-estuarine environment at late Miocene times in Urumaco.

Source: Carrillo-Briceño et al. (2015b). Artwork: Jorge González, 2015.

CONTENTS

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SUMMARY

The aim of this study is to investigate the Neogene chondrichthyan fauna from Tropical America, based on the documentation of fossil assemblages from different localities of Eastern Pacific and Western Atlantic. Fifteen new assemblages from the Caribbean (Colombia, Panama and Venezuela), Western Atlantic coast (Brazil, in prep.), and Eastern Pacific (Ecuador) were studied, and analyses of their associated paleoenvironments were presented. In Chapter 1, a brief introduction to the evolutionary history of chondrichthyans, a brief survey of the extant and Neogene diversity from Tropical America, and the outline of the project are presented.

The elasmobranch fauna from Eastern Pacific described in Chapter 2, included a taxonomic revision of four assemblages from the Miocene-Pleistocene of Ecuador (Angostura, Onzole, Canoa and Jama formations of Bordón and Manabí basins), resulting in the most diverse paleodiversity known from that region. This study resulted in the description of a new deep water species of frilled shark †*Chlamydoselachus landinii* and other 29 taxa with either deep or shallow water affinities, suggesting paleoenvironments associated with a short platform shelf bordering a deep margin.

Chapter 3 describes the elasmobranch fauna of two members of Chagres Formation, which is the youngest deposit of the Panama Canal Basin in the Caribbean side. A paleodiversity of 30 taxa from both the Rio Indio and Chagres Sandstone Members is reported, including 18 new records for Panama and four for Tropical America. The performed paleobathymetry analysis from the Rio Indio Member suggests a shallow water environment, whereas the assemblage from the Chagres Sandstone Member is dominated by taxa with oceanic affinities, suggesting 200-300 m water depths.

In Chapter 4, 21 taxa of sharks and rays are reported from the Socorro (Middle Miocene), Urumaco (late Miocene) and Codore (late Miocene-early Pliocene) formations located in western Venezuela. These geological units correspond to the "Urumaco sequence", one of the most significant vertebrate fossiliferous areas from the Neogene of the Northern part of South America. The elasmobranch assemblages include the description of a new carcharhiniform species †*Carcharhinus caquetius* sp. nov., and a detailed taxonomic revision of a high number of well-preserved three-dimensional fossil sawfish rostra (*Pristis*: Rajiformes). We referred to the habitat preferences of the living representatives of fossil chondrichthyan present in the assemblages to reconstruct marine shallow waters and estuarine habitats for this assemblage.

Chapters 5 and 6 concern the taxonomic description of two elasmobranch assemblages of the early Miocene of Colombia and Venezuela, respectively. The assemblage from Colombia comes from the Aquitanian deposits of the Uitpa Formation in the La Guajira Peninsula, providing a unique glimpse into the Caribbean biodiversity at the onset of the Neogene. Thirteen taxa were recovered, and the assemblage was used to conduct a paleoenvironmental and paleobathymetric analysis. The estimation of paleobathymetry suggests that the Uitpa Formation was likely accumulated in a depth of 100 to 200 m. This suggests a rapid increase in relative sea level or basin deepening, providing new insights into the possible causes of marine biota changes in the Cocinetas Basin during the Oligocene/Miocene transition. The assemblage from Venezuela comes from Burdigalian to ?early Langhian deposits of the Cantaure Formation, located in the Paraguaná Peninsula. The fauna is characterized by 39 sharks and ray species, including 15 previously unreported taxa for Venezuela and six for Tropical America, representing one of most diverse assemblages from early Neogene of the Americas. This fauna is characterized by a predominance of

benthopelagic sharks with piscivorous feeding preferences, followed by durophagous/cancritrophic feeders. Habitat preferences, paleobathymetric analyses, and other associated invertebrate and vertebrate assemblages, support the hypothesis that the Cantaure Formation was deposited in a high productivity, insular inner-middle shelf environment.

Preliminary results reveal that throughout the Neogene the chondrichthyan paleodiversity of Tropical America has not remained constant, especially in shark genera, in both Eastern Pacific and Western Atlantic. In spite of the exponential increase in data presented in this thesis, the Neogene record of chondrichthyans is still too incomplete as to provide a solid test of the abiotic variables that affected the evolution of these animals. Our survey not offers a direct biostratigraphic inference to support any of the timings for the definitive closure of the Panama Isthmus. However, clues related with possible consequence of "post-Isthmus" environmental changes can be observed. The analysis reveal regional or complete extirpation, especially during late Miocene-Pliocene, where at least 18 shark/ray taxa (mainly neritic/epipelagic species) from the Eastern Pacific and Western Atlantic were affected.

Keywords: Tropical America, Eastern Pacific, Western Atlantic, Caribbean Sea, Brazil, Colombia, Ecuador, Panamá, Venezuela, Paleodiversity, Paleoenviroments, Central American Seaway, Fossil, Sharks, Rays.

ZUSAMMENFASSUNG

Das Ziel dieser Arbeit ist es die Neogene Chondrichthyes-Fauna aus dem tropischen Amerika, basierend auf der Dokumentierung von Fossilienvergesellschaftungen aus verschiedenen Lokalitäten vom östlichen Pazifik und dem westlichen Atlantik, zu untersuchen. Fünfzehn neue Fossilienvergesellschaftungen von der Karibik (Kolumbien, Panama und Venezuela), der westlichen Atlantikküste (Brasilien, in Vorbereitung), und des östlichen Pazifiks (Ecuador) wurden untersucht und Analysen ihrer assoziierten Palaeoumwelt wurden präsentiert. Eine kurze Einleitung in die Evolutionsgeschichte der Chondrichthyes, eine Übersicht über die heutige und die Neogene Diversität des tropischen Amerikas und ein Umriss über das gesamte Projekt werden in Kapitel 1 dieser Arbeit gegeben.

Die in Kapitel 2 beschriebene Elasmobranchier-Fauna aus dem östlichen Pazifik beinhaltete die taxonomische Revidierung von vier Fossilienvergesellschaftungen aus dem Miozän-Pleistozän von Ecuador (Angostura-, Onzole-, Canoa- und Jama-Formation aus dem Bordón-, respektive Manabí-Becken) und resultierte in der höchsten Palaeodiversität aus dieser Region. Aus dieser Arbeit resultierte die Beschreibung einer neuen Tiefseeart der Kragenhaie †*Chlamydoselachus landinii* und 29 zusätzlichen Taxa mit Affinitäten zu entweder Tiefen- oder Flachwasser. Diese Affinitäten weisen auf ein Kontinentalhang-Environment hin.

In Kapitel 3 wird die Elasmobranchier-Fauna aus zwei Members der Chagres-Formation, welche die jüngste Ablagerung des Panamkanal-Beckens auf der karibischen Seite ist, beschrieben. Die Palaeodiversität bestand aus 30 Taxa vom Rio Indio und dem Chagres Sandstone Member und beinhaltete 18 neue Taxa von Panama und vier neue Taxa aus dem tropischen Amerika. Die Analyse der Palaeobathymetrie von der Rio Indio Member deutete auf ein Flachwasser-Environment hin, während die Fossiliengemeinschaft aus dem Chagres

Sandstone Member von Taxa mit ozeanischen Affinitäten dominiert wurde und auf eine Wassertiefe von 200 bis 300 Meter hindeutete.

In Kapitel 4 wurde von 21 Hai- und Rochen-Taxa aus der Socorro- (mittleres Miozän), Urumaco- (spätes Miozän) und Codore- (spätes Miozän-frühes Pliozän) Formation aus dem Westen Venezuelas berichtet. Diese geologische Einheit entspricht der "Urumaco Sequenz", welche eine der fossilienreichsten Gebiete des Neogens aus dem nördlichen Südamerika ist. Basierend auf der Elasmobranchier-Fauna wurde eine neue Art der Carcharhiniformes †*Carcharhinus caquetius* sp. nov. beschrieben und die Taxonomie der Sägefische (*Pristis*: Rajiformes) anhand von vielen dreidimensional erhaltenen Rostren detailliert revidiert. Anhand der Habitatspräferenzen von heute noch lebenden Vertretern, die in den Fossilienvergesellschaftungen vorkamen, konnte ein marines Flachwasser und estuarines Habitat rekonstruiert werden.

Kapitel 5 und 6 befassen sich mit der taxonomischen Beschreibung von zwei fossilen Elasmobranchier-Vergesellschaftungen aus dem frühen Miozän von Kolumbien und Venezuela. Das Material aus Kolumbien stammt aus den Aquitanium-Ablagerungen von der Uitpa Formation in der La Guajira Peninsula und gibt einen einzigartigen Einblick in die karibische Biodiversität zu Beginn des Neogens. Dreizehn Taxa wurden gefunden und das Palaeoenvironment und die Palaeobathymetrie wurden anhand der Fossilienvergesellschaftungen analysiert. Die Schätzung der Palaeobathymetrie deutet darauf hin, dass die Uitpa Formation in einer Tiefe von 100 bis 200 Metern akkumuliert wurde. Dies deutet auf einen schnellen Anstieg des relativen Meeresspiegels oder eines Absenkens des Beckens hin, was zu neuen Erkenntnissen über die möglichen Ursachen der Veränderungen in der marinen Biota im Cocinetas-Becken während des Oligozän/Miozän-Übergangs führt. Die Fossilienvergesellschaftungen aus Venezuela stammt aus den Burdigalium bis ?frühen

Langhien-Ablagerungen der Cantaure Formation, welche sich in der Paraguaná Peninsula befindet. Die Fauna ist charakterisiert durch 39 Hai-und Rochenarten, inklusive 15 zuvor unbekannten Taxa aus Venezuela, respektive sechs aus dem tropischen Amerika und repräsentieren somit eine der diversesten Fossilienvergesellschaftungen aus dem frühen Neogen von ganz Amerika. Die Fauna ist charakterisiert durch die Dominanz von benthopelagischen Haien mit piscivoren Nahrungspräferenzen, gefolgt von durophagen/cancritrophen Haiarten. Habitatspräferenzen, palaeobathymetrische Analysen und assoziierte Invertebraten- und Vertebraten-Vergesellschaftungen unterstützen die Hypothese, dass die Cantaure Formation in einem hochproduktiven, Inselähnlichem Environment abgelagert wurde.

Die vorläufigen Resultate dieser Arbeit zeigen, dass die Palaeodiversität der Chondrichthyes des tropischen Amerikas, besonders die Haigattungen im östlichen Pazifik und westlichen Atlantik, während des Neogens nicht konstant geblieben sind. Trotz des exponentiellen Anstiegs der Daten, die in dieser Arbeit präsentiert werden, ist der Fossilbericht der Neogenen Knorpelfische immer noch zu lückenhaft um einen solide Überprüfung der abiotischen Faktoren, die die Evolution dieser Tiere beeinflusst hat, zu liefern. Aus unserer Untersuchung lässt sich kein direkter biostratigraphischer Rückschluss ziehen um den Zeitpunkt der definitiven Schliessung des Panama Isthmus zu bestätigen. Jedoch konnten mögliche Konsequenzen durch die "post-Isthmus" Umweltveränderungen beobachtet werden. Die Analyse weist auf ein regionales oder vollständiges Aussterben von Taxa im tropischen Amerika hin: Besonders während des späten Miocene-Pliocene verschwanden mindestens 18 Hai- und Rochen-Taxa (hauptsächlich neritische/epipelagische Arten) aus dem östlichen Pazifik und dem westlichen Atlantik.

Schlüsselworte: Tropisches Amerika, östlicher Pazifik, westlicher Atlantik, karibisches Meer, Brasilien, Kolumbien, Ecuador, Panama, Venezuela, Palaeodiversität, Palaeoenvironment, Zentralamerkanischer Seeweg, Fossilien, Haie, Rochen.

AUTHOR CONTRIBUTIONS

Excluding chapters one (Introduction) and seven (Conclusion and Future Perspectives), the remaining chapters and appendices of this thesis have been published in peer-reviewed journals.

CHAPTER 1

Author: Carrillo-Briceño J.D.

CHAPTER 2

Fossil Chondrichthyes from the central eastern Pacific Ocean and their paleoceanographic significance.

Publication: 2014, Journal of South American Earth Sciences, 51: p. 76–70.

Authors: Carrillo-Briceño J.D., Aguilera O.A., and Rodríguez F.

Contributions: designed research (JDCB, OAA), data collection (JDCB, OAA), data analysis (JDCB, OAA), photography (OAA, FR), figures and tables (JDCB), wrote paper (JDCB, OAA).

CHAPTER 3

A new Late Miocene chondrichthyan assemblage from the Chagres Formation, Panama.

Publication: 2015, Journal of South American Earth Sciences, 60: p. 56–70.

Authors: Carrillo-Briceño J.D., De Gracia C., Pimiento C., Aguilera O.A., Kindlimann R., Santamarina P., and Jaramillo C.

Contributions: designed research (JDCB, CD, CJ), data collection (JDCB, CD, OAA), data analysis (JDCB, CD, RK, CJ), photography (JDCB, CD,), figures and tables (JDCB, CD), wrote paper (JDCB, CD), editing of the manuscript (JDCB, CD, CJ, CP).

CHAPTER 4

Sawfishes and Other Elasmobranch Assemblages from the Mio-Pliocene of the South Caribbean (Urumaco Sequence, Northwestern Venezuela).

Publication: 2015, PLoS ONE, 10(10): e0139230.

Authors: Carrillo-Briceño J.D., Maxwell E., Aguilera O.A., Sánchez R., and Sánchez-Villagra M.R.

Contributions: designed research (JDCB, EM), data collection (JDCB, EM, OAA, RS), data analysis (JDCB, EM), photography (JDCB), figures and tables (JDCB), wrote paper (JDCB, EM, MRSV), editing of the manuscript (JDCB, EM, OAA, MRSV).

CHAPTER 5

A new early Miocene (Aquitanian) Elasmobranchii assemblage from the La Guajira Peninsula, Colombia.

Publication: 2016, Ameghiniana 53: p. 77–99.

Authors: Carrillo-Briceño J.D., Argyriou T., Zapata V., Kindlimann R., and Jaramillo C.

Contributions: designed research (JDCB, CJ), data collection (JDCB, VZ), data analysis (JDCB, TA; CJ, RK), photography (JDCB, VZ), figures and tables (JDCB, TA), wrote paper (JDCB, TA, CJ), editing of the manuscript (JDCB, TA, CJ).

CHAPTER 6

An Early Neogene Elasmobranch fauna from the southern Caribbean (Western Venezuela).

Publication: 2016, Paleontologia Electronica.

Authors: Carrillo-Briceño J.D., Aguilera O.A., De Gracia C., Aguirre-Fernández G., Kindlimann R., and Sánchez-Villagra M.R.

Contributions: designed research (JDCB, OAA), data collection (JDCB, OAA, GAF, MESV), data analysis (JDCB, CD, RK), photography (JDCB), figures and tables (JDCB), wrote paper (JDCB), editing of the manuscript (JDCB, GAF, MRSV).

APPENDIX I

Late Neogene elasmobranch fauna from the Coquimbo Formation, Chile.

Publication: 2015, Revista Brasileira de Paleontologia, 18(2): p. 261–272.

Authors: Staig F., Hernández S., López P., Villafaña J.A., Varas C., Soto L.P., and Carrillo-Briceño, J.D.

Contributions: designed research (FS, PS, JAV), data collection (FS, PS, JAV, PLS, JDCB), data analysis (FS, JAV, PLS, JDCB), photography (FS, JAV), figures and tables (JAV), wrote paper (FS, PS, JAV, JDCB), editing of the manuscript (FS, PS, JAV, JDCB).

APPENDIX II

The Path towards Endangered Species: Prehistoric Fisheries in Southeastern Brazil. Publication: 2016, PLoS ONE, 11(6): e0154476.

Authors: Lopes M.S., Pereira-Bertucci T.C., Rapagnã L., Tubino R.A., Monteiro-Neto C., Tomas ARG, Tenório M.C., Lima T., Souza R., Carrillo-Briceño J.D., Haimovici M., Macario K., Carvalho C., Aguilera-Socorro O.A.

Contributions: designed research (MSL, TCPB, OAAS), data collection (MSL, TCPB, OAAS), data analysis (MSL, TCPB, LR, RAT, CMN, ARGT, MCT, TL, RS, JDCB, MH, KM, CC, OAAS), photography (MSL, TCPB, OAAS, JDCB), figures and tables (MSL, TCPB, OAAS, JDCB), wrote paper (MSL, TCPB, OAAS), editing of the manuscript (MSL, TCPB, LR, RAT, CMN, ARGT, MCT, TL, RS, JDCB, MH, KM, CC, OAAS).

CHAPTER 1

Introduction

Tiger shark *Galeocerdo cuvier*. Artwork: Jorge González, 2015

1. Introduction

1.1 A brief introduction to the evolutionary history and extant diversity of chondrichthyans

Living chondrichthyan diversity is composed of thirteen 'orders' (Figure 1), separated in two big groups, the Elasmobranchii, that includes sharks and rays, and the Holocephali, represented exclusively by the chimaeras (Compagno et al., 2005a; Klimley, 2013). With a worldwide distribution, in both freshwater and marine environments, this diversity has been referred to 503 species of sharks, 699 species of rays and 49 species of chimaeras (Klimley, 2013). In the future more species are likely to be discovered as the deep waters of the world's oceans become better explored.

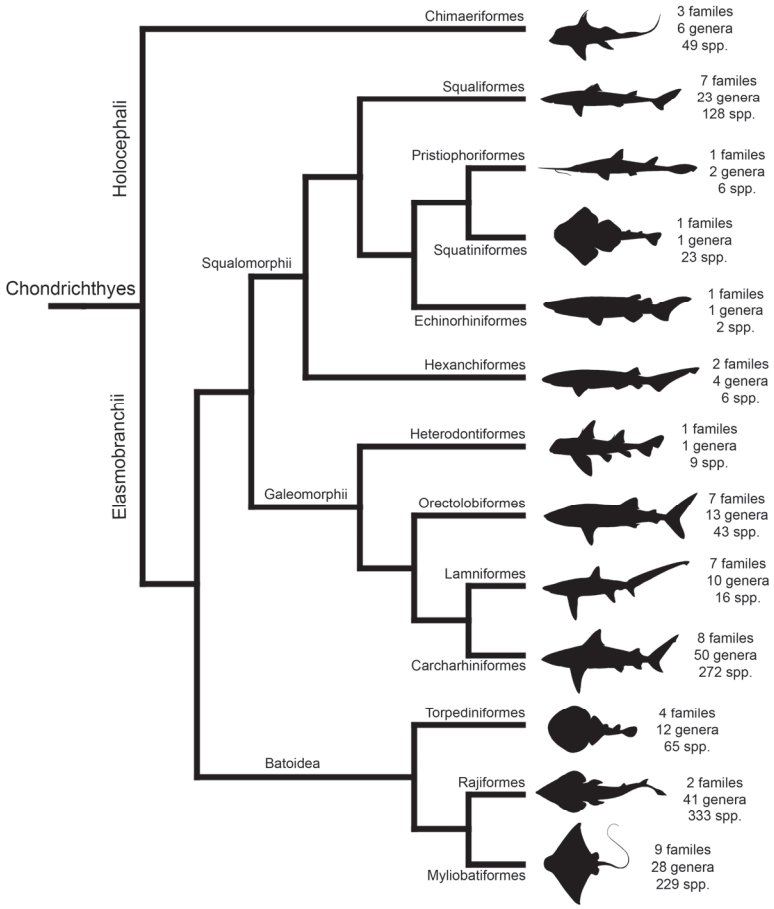

Figure 1. Diversity and phylogenetic hypothesis of living chondrichthyans. Based on Naylor et al. (2012), Aschliman et al. (2012), and Klimley (2013).

The chondrichthyan evolutionary history may have undergone two major episodes of adaptive radiation (Figure 2), the first during late Silurian and Devonian (Brazeau and Friedman, 2015), resulting in sharks that broadly resemble modern genera but with a more plesiomorphic skeleton (Carroll, 1988). By the early Carboniferous, chondrichthyans underwent a second major radiation process, where many 'families' and major clades appeared, including holocephalans (Jong, 2011; Brazeau and Friedman, 2015). This radiation continued throughout the Mesozoic; by the end of this era most of the modern chondrichthyan 'orders' had appeared (e.g. Jong, 2011; Cappetta, 2012).

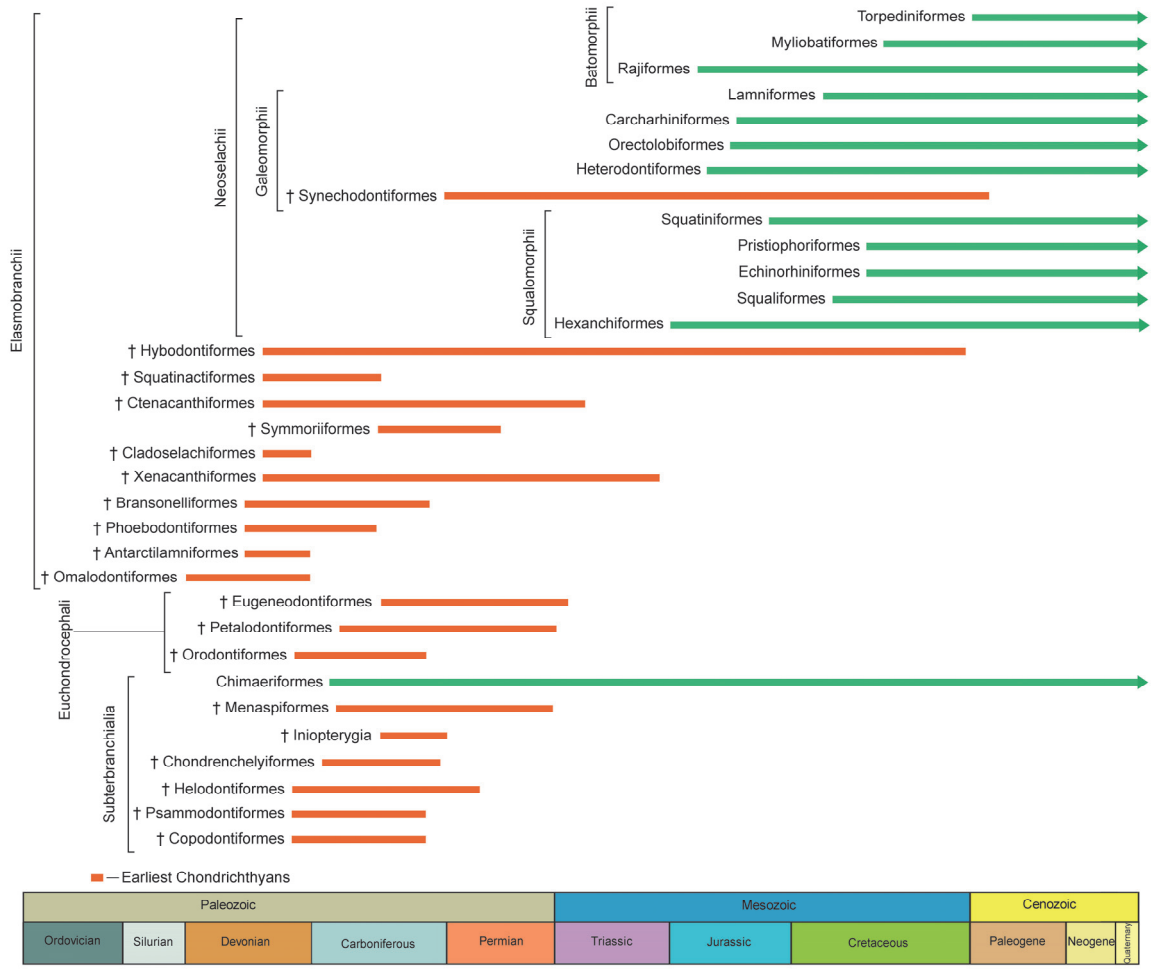

Figure 1. Stratigraphic range of major chondrichthyan clades ('orders'). Based on Stahl (1999), Ginter (2010), and Cappetta (2012).

The evolution of chondrichthyans is documented paleontologically principally by fossil vertebrae, teeth, spines and dermal denticles, besides some exceptionally preserved specimens consisting of cranial elements or the whole body. The earliest fossil evidence of chondrichthyans is in the form of isolated dermal denticles, specimens found in rock deposits of the late Ordovician period (Figure 1), with an age of 455 million years ago (Ma.) (Maisey, 1996; Cuny, 2013; Klimley, 2013). According to Jong (2011), the fact these dermal denticles occur in this time without associated fossilized teeth, suggest that these early "protosharks" may not necessarily have had teeth. First shark teeth appear in the fossil record at the beginning of the Devonian period (418 Ma.), and they were clearly derived from dermal denticles, which had become concentrated by this time along the margin of the jaw (Klimley, 2013, p. 15).

1.2 The Neogene marine chondrichthyan faunas from Tropical America

The "Neogene" is a geological period which following the International Commission on Stratigraphy (ICS) began about 23 Ma. and ended 2.58 Ma.; it is sub-divided into two epochs, the Miocene and Pliocene (Figure 2). This period was a time when the world climate was warmer, producing for example sea level changes (Zachos et al., 2001). At the time, the America landmass had a similar geographic position to the recent one (Santos et al., 2004), but the northern and southern continental masses were separated by a connection between the Pacific and Atlantic Oceans called the "Central America Seaway" (Montes et al., 2012; Coates and Stallard, 2013). At the end of the Neogene, large scale geological processes, including the closure of the Central American Seaway and the rise of the Panamanian Isthmus (Figure 2), were completed (Woodburne, 2010; Montes et al., 2012, 2015; Coates and Stallard, 2013). This resulted in a massive terrestrial faunal exchange between North America

and South America, the Great American Biotic Interchange (Woodburne, 2010, Carrillo et al., 2015). The land bridge played also the role of a marine barrier, inducing environmental changes on the Pacific and Atlantic oceans, creating contrasting ecosystems through differential extinction and diversification, especially in the Tropical America region (Leigh et al., 2014).

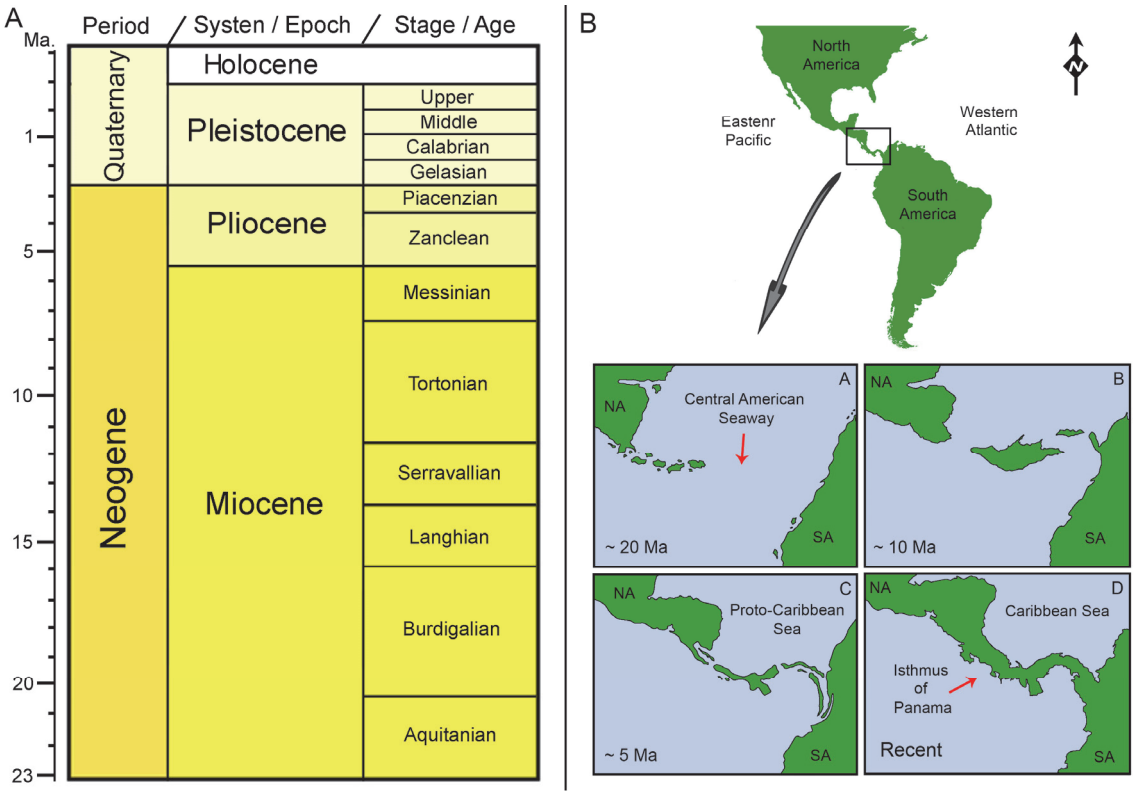

Figure 2. Neogene chronostratigraphy (A) and the rise of the Isthmus of Panama (B); based on International Chronostratigraphic Chart 2015 (http://www.stratigraphy.org/index.php/ics-chart-timescale), and modified after Carrillo-Briceño (2015) and based on O'Dea et al. (2007b); respectively.

Tropical America (Neotropics) refers here to the geographical continental and marine areas of the western hemisphere located between the Tropic of Cancer (23° 27' N) and the Tropic of Capricorn (23° 27′ S) (Figure 3). This vast marine region is environmentally

heterogenic and ecologically complex, supporting a high marine diversity (e.g. Miloslavich et al., 2011). Marine areas of Tropical America have a well-known chondrichthyan diversity in both Eastern Pacific and Western Atlantic zones, which represents a valuable commercial resource (Carpenter, 2002; Compagno et al., 2005b; Fowler et al., 2005). The known Tropical America's extant chondrichthyan diversity is characterized by a total of 276 species of chimaeras, sharks and rays (Eastern Pacific: 145 spp.; Western Atlantic 181 spp.), representing the highest for the group in the Americas (Figure 3). Comparing the Eastern Pacific and Western Atlantic, a clear differential pattern emerge (Figure 4). This pattern was surely influenced by the geological and oceanographic events that occurred in the region after the final closure of the Isthmus of Panama (e.g. O'Dea et al., 2007a; Coates, and Stallard, 2013; Leigh et al., 2014).

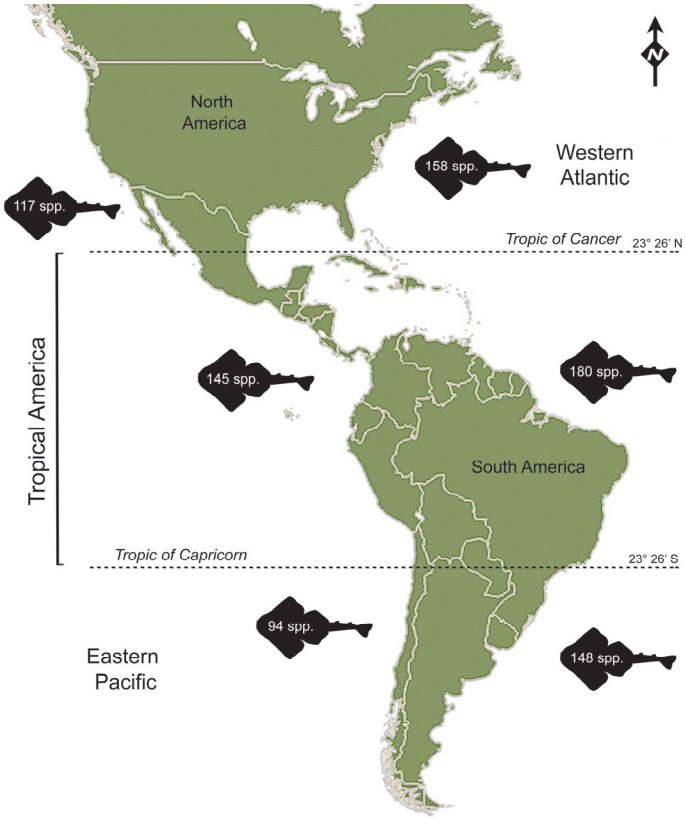

Figure 3. Tropical America and chondrichthyan diversity of the Americas. Total number of species include chimaeras, sharks and rays. From Carrillo-Briceño and Sánchez-Villagra (in prep).

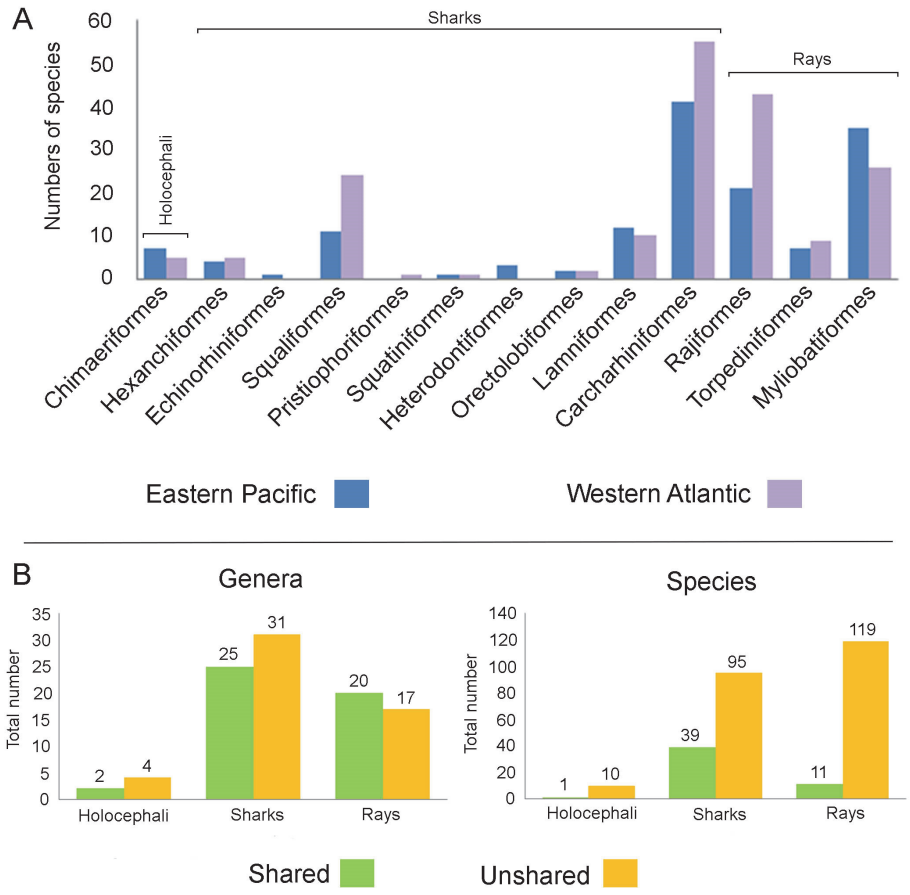

Figure 4. Chondrichthyan diversity of Tropical America. A. Total number of species by 'orders'. B. Shared/Unshared genera and species in both the Eastern Pacific and Western Atlantic. From Carrillo-Briceño and Sánchez-Villagra (in prep).

The origin and distribution pattern of this Tropical America chondrichthyan diversity is still somewhat uncertain, in part due to the fragmentary and incompletely studied Neogene fossil record. Some previous works have made contributions to document fossil chondrichthyan palaeodiversity from Tropical America, with described assemblages from: Barbados (Casier, 1958, 1966), Brazil (Santos and Travassos, 1960; Santos and Salgado, 1971; Reis, 2005; Costa et al., 2009), Costa Rica (Laurito, 1999); Cuba (Iturralde-Vinent et al., 1996; MacPhee et al., 2003), Southern Mexico (González-Rodríguez et al., 2013), Panama

(Pimiento et al., 2013a, 2013b), Peru (Kindlimann, 1990; Alván et al., 2007), Trinidad (Leriche, 1938), The Grenadines (Portell et al., 2008) and Venezuela (Leriche, 1938; Sánchez-Villagra et al., 2000; Aguilera, 2010; Aguilera and Rodrigues de Aguilera, 2004; Aguilera and Lundberg, 2010).

1.3 Chondrichthyan dental characters and the used terminology

Teeth, dermal denticles, vertebrae, fin spines, rostra, among other hard elements, are common in the fossil record of chondrichthyans. Due to the fact that selachians have a polyphyodont dentition, in which dental elements are replaced throughout life (Klimley, 2013; Pough et al., 2013), teeth are usually the most common chondrichthyan remains found in Neogene rocks (e.g. Cappetta, 2012), and their role as diagnostic elements allows for accurate taxonomic comparisons. Shark and ray teeth chemical composition is similar to that of dermal denticles, consisting mainly of mineralized tissue, dentine, interspersed with blood vessel and surrounded by highly mineralized enameloid on the crown of the tooth (Klimley, 2013). Tooth development and replacement in sharks and rays have been the subject of many studies (e.g. Cappetta, 2012, p. 10), and the study of their morphological changes in geological time provide the basis understanding of the evolution of these diverse fish groups (Underwood et al., 2015).

There are diagnostic characters for identifications of an isolated tooth based on its morphology, including size, shape and thickness of the crown and root (Cappetta, 2012). Taking under consideration dental characters in chondrichthyans can serve for generic and specific identifications. Some exceptions where taxonomic problems cannot be solved include a poor preservation of the fossil specimens and/or the biases or uncertainties resulting from

ontogenetic variation or jaw position. In the studied assemblages from Tropical America, the fossil samples are represented mainly by isolated teeth. Some other fossil elements, such as sawfish rostra (including rostral denticles), vertebrae and dermal denticles were also found in a minor proportion. The dental terminology (including measurements, heterodonty, adaptative dental types, root vascularization, jaw position and tooth histology) used to describe these assemblages from tropical America, follows Cappetta (2012).

1.4 Aims and overview

The extant Tropical America's chondrichthyan diversity (Figures 3-4) must have greatly affected by environmental changes occurring in both Eastern Pacific and Western Atlantic regions after the definitive closure of the Panana Isthmus at the end of the Neogene (e.g. O'Dea et al., 2007a; Coates and Stallard, 2013). This land-bridge played an important role as a marine barrier, probably inducing to a regional or completes extirpation and or extinctions of many chondrichthyan taxa, as well as the origin of species adapted to the new environmental conditions. To understand the current diversity, two important questions are postulated: a) what was the chondrichthyan paleodiversity in Tropical America before and after the rise of the Panama Isthmus? b) Did the new marine post-isthmus environmental differences in both oceans played an important role for chondrichthyan divergence and speciation? Despite all previous efforts in the study of the fossil chondrichthyans from Tropical America, still the lack of a solid paleontological documentation does not allow for an understanding of the impact of these regional ecological and biogeographic changes (e.g. O'Dea et al., 2007a; Coates and Stallard, 2013; Montes et al., 2015).

The aim of this study is to investigate the Neogene chondrichthyan fauna from Tropical America, based on the documentation of fossil assemblages with shallow and deep-water affinities from both sides of the Panamanian Isthmus. We studied fifteen new chondrichthyan assemblages from the Caribbean (Colombia, Panama and Venezuela), Western Atlantic coast (Brazil, in prep.), and Eastern Pacific (Ecuador), presenting a comprehensive interpretation of their associated paleoenvironments.

In chapter 2, a taxonomic revision of four elasmobranch assemblages from the Miocene-Pleistocene of Ecuador (Angostura, Onzole, Canoa and Jama formations of Bordón and Manabí basins) is provided, resulting in the most diverse paleodiversity known from the Eastern Pacific coast of Tropical America. This study reveals the presence of at least 30 taxa, including species with deep and shallow waters affinities which suggest paleoenvironments associated with a short platform shelf bordering a deep margin. The new deep water species †*Chlamydoselachus landinii* sp. nov. was described.

Chapter 3 includes the description of two new assemblages from both the Rio Indio and Chagres Sandstone Members of the Chagres Formation. This unit corresponds with youngest deposits of the Panama Canal Basin, and their paleodiversity includes 18 new fossil records for Panama and four for Tropical America. Herein it is presented a comprehensive interpretation of the paleoenvironments of assemblages of the Chagres Formation, for which a paleobathymetry analysis based on the modern water depth preference of extant chondrichthyan taxa was performed. The assemblage from the Rio Indio Member is characterized by taxa with neritic affinities, suggesting depths <100 m, whereas the assemblage from the Chagres Sandstone Member is dominated by taxa with oceanic affinities, suggesting 200-300 m water depths.

Chapter 4 is concerned with one of the most significant vertebrate fossiliferous areas from the Neogene of the Northern part of South America "The Urumaco sequence". This stratigraphic sequence is located in western Venezuela, and preserves a wide range of fossil vertebrate associated to different paleoenvironments including terrestrial, riverine, lacustrine and marine facies. Herein, 21 taxa of sharks and rays were referred from the Socorro (Middle Miocene), Urumaco (late Miocene) and Codore (late Miocene-early Pliocene) formations. The assemblages include the description of a new carcharhiniform species †*Carcharhinus caquetius* sp. nov. The high number of well-preserved 3D fossil sawfish rostra (*Pristis*: Rajiformes), allowed a detailed taxonomic revision of these specimens, referring those in the context of the global Miocene record of *Pristis* as well as extant species. Using the habitat preference of the living representatives, fossil chondrichthyan assemblages from the Urumaco sequence are evidence for marine shallow waters and estuarine habitats.

Chapter 5 comprises the first taxonomic description for a chondrichthyan assemblage from Colombia. This elasmobranch assemblage is coming from the earliest Miocene (Aquitanian) deposits of the Uitpa Formation in the La Guajira Peninsula, providing a unique glimpse into the Caribbean biodiversity at the onset of the Neogene. Thirteen taxa were recovered, and the assemblage was used to conduct a paleoenvironmental and paleobathymetric analysis. The estimation of paleobathymetry suggests that the Uitpa Formation was likely accumulated in a depth of 100 to 200 m. This suggests a rapid increase in relative sea level or basin deepening, providing new insights into the possible causes of marine biota changes in the Cocinetas Basin during the Oligocene/Miocene transition.

Chapter 6 continues the description of assemblages from southern Caribbean, this time with a focus in the Cantaure Formation (Burdigalian to ?early Langhian), Western Venezuela. Here a taxonomic study of the elasmobranch fauna and their significance for

paleoenvironmental and paleoecological inferences is presented. The assemblage is represented by 39 shark and ray species, including 15 previously unreported taxa for Venezuela and six for Tropical America, Cantaure being thus one of most diverse assemblages from early Neogene of the Americas. The fauna is characterized by a predominance of benthopelagic sharks with piscivorous feeding preferences, followed by durophagous/cancritrophic feeders. Habitat preferences, paleobathymetric analyses, and other associated invertebrate and vertebrate assemblages, support the hypothesis that the Cantaure Formation was deposited in a high productivity, insular inner-middle shelf environment.

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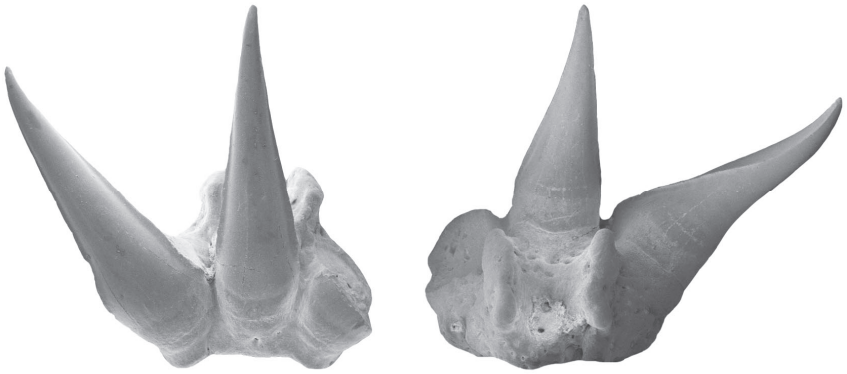
CHAPTER 2

Fossil Chondrichthyes from the central Eastern Pacific Ocean and their paleoceanographic significance



Frilled shark †*Chlamydoselachus landinii*

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Fossil Chondrichthyes from the central eastern Pacific Ocean and their paleoceanographic significance

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ABSTRACT

The study of the chondrichthyan fauna from the Angostura, Onzole, Canoa and Jama formations, in the Neogene of Bordón and Manabí basins, Ecuador, reveals the presence of 30 taxa, including the deep water shark †*Chlamydoselachus landinii* sp. nov. The assemblages are dominated by tropical shallow and deep water chondrichthyans, suggesting paleoenvironments associated with a short platform shelf bordering a deep margin. These assemblages are the most diverse shark and ray association known from the Tropical Central Eastern Pacific Ocean in the South American coastal basin, and provide new information on the paleoecology and paleodiversity of Neogene chondrichthyans.

1. Introduction

Fossil chondrichthyan assemblages from the eastern Pacific Ocean are still poorly known in spite of several publications on the subject, including: Longbottom (1979) and Aguilera et al. (2011) on Ecuador; De Muizon and Devries (1985), Kindlimann (1990), Apolín et al. (2004) and Avalán et al. (2007) on Perú; Long (1993a), Suárez and Marquardt (2003), Suárez et al. (2006) and Carrillo-Briceño et al. (2013) on Chile; Laurito (2004), and Laurito and Valerio (2008) on Central America, and Long (1993b), González-Barba and Thies (2000), and Boessenecker (2011) on North America. These previous contributions are not uniform in terms of sampling and geochronological control, preventing comparative quantitative analyses among faunas. However, the faunal assemblages along the tropical eastern Pacific coast have been the subject of studies about faunal distribution in Tropical America and the proto-Caribbean area (Iturralde-Vinent and MacPhee, 1999; Landini et al., 2002a, 2002b; Aguilera et al., 2011; Carnevale et al., 2011).

In terms of regional relevance, the central eastern Pacific Ocean represents a geographic and oceanographic complex influenced by geologic and tectonic events along the Panamanian Atlantic–Pacific seaway (Hoernle et al., 2002; Pindell et al., 2005), related to the uplift of the Isthmus of Panama (Coates and Obando, 1996; O'Dea et al., 2007; Coates and Stallard, 2013), the Andean uplift (Garzione et al., 2008; Martinoid et al., 2010), the Ecuadorian subduction, the submarine trench system (Lonsdale, 1978; Ratzov et al., 2010) and the oceanographic dynamic (Fiedler and Talley, 2006) derived in successions of neritic to depth sea paleoenvironment changes. Longbottom (1979) described the early chondrichthyan fauna assemblage from the Miocene of the Onzole Formation and Aguilera et al. (2011) reported the presence of additional Miocene-Pleistocene taxa from the Angostura, Onzole and Jama formations from Ecuador. Teleostean records from the Neogene basin in Ecuador are known from otoliths reported from the Onzole and Canoa formations (Landini et al., 2002a, 2002b; Aguilera et al., 2011; Carnevale et al., 2011).

In this work we provide a taxonomic revision of the chondrichthyan fauna from Ecuador, resulting in an increased fossil record for the region and a better understanding of the Neogene shark and ray associations in Tropical America, especially along the eastern Pacific coast of South America.

2. Methods

The chondrichthyan assemblages (Table 1) were collected from nine localities (Fig. 1) of four Neogene geological units in Ecuador, including: Cayapas River [Telembí (0° 58′ 57″ N, 78°51′ 42″ W)],

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CHAPTER 3

A new Late Miocene chondrichthyan assemblage from the Chagres Formation, Panama

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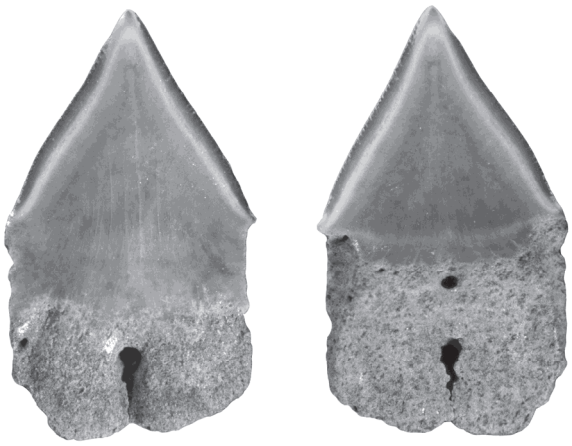

Cookiecutter shark *Isistius* sp.

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A new Late Miocene chondrichthyan assemblage from the Chagres Formation, Panama

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ABSTRACT

The lLate Miocene Chagres Formation from northern Panama contains the youngest outcrops of the Panama Canal Basin. Here we report two chondrichthyan assemblages that include 30 taxa from both the Rio Indio and Chagres Sandstone Members of the Chagres Formation. We report 18 new fossil records for Panama and four for tropical America, constituting the most diverse chondrichthyan association for the Cenozoic of Panama. We performed a paleobathymetry analysis based on the modern water depth preference of extant chondrichthyan taxa. The assemblage from the Rio Indio Member is characterized by taxa with neritic affinities, suggesting depths <100 m, whereas the assemblage from the Chagres Sandstone Member is dominated by taxa with oceanic affinities, suggesting 200–300 m water depths. The Chagres Sandstone Member could have accumulated at the edge of a platform–upper slope, bordered by a deep oceanic margin.

1. Introduction

Panamanian sedimentary basins preserve an extensive Neogene fossil record of marine biota useful for understanding the evolution of the Isthmus of Panama. The isthmus was formed by complex tectonic processes that isolated the Atlantic from the Pacific Ocean and connected North and South America, precipitating major biogeographic, oceanographic, and environmental changes (Coates and Obando, 1996; Woodburne, 2010; Coates and Stallard, 2013; Leigh et al., 2013). The formation of the Isthmus of Panama was completed during the Pliocene, between 4.2 and 3.5 Ma (Duque-Caro, 1990; Coates et al., 1992, 2003, 2004; Coates and Obando, 1996; Haug and Tiedemann, 1998; Bartoli et al., 2005; Woodburne, 2010; Haug et al., 2001; Coates and Stallard, 2013). Additional geological evidence suggests that the rise of the isthmus was considerably older and more complex, with an initial collision between South America and the Panama Block between 25 and 23 Ma (Farris et al., 2011; Montes et al., 2012a, 2012b). By 20 Ma, Panama would have been a peninsula connected to North America (MacFadden et al., 2010; Montes et al., 2012a; Rincon et al., 2012), with an oceanic pathway between Panama and South America, the Central American Seaway (CAS, defined here as the deep oceanic seaway along the tectonic boundary of the South American plate and the Panama microplate), connecting the Pacific and Atlantic Oceans (Montes et al., 2012a, 2012b). By 10 Ma, a full closure of CAS had occurred, ending the exchange of deep and intermediate waters between the Caribbean and the Pacific (Coates et al., 2004; Montes et al., 2012a; Sepulchre et al., 2014). However, shallow-water exchange continued between the two oceans along pathways other than CAS, allowing the migration of chondrichthyans between basins (Pimiento et al., 2013b), until the complete rise of the Isthmus at 3.5 Ma (Duque-Caro, 1990; Haug and Tiedemann, 1998; Haug et al., 2001; Coates et al., 1992, 2003, 2004; Coates and Stallard, 2013). Ultimately, the formation of the Isthmus of

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CHAPTER 4

Sawfishes and Other Elasmobranch Assemblages from the Mio-Pliocene of the South Caribbean (Urumaco Sequence, Northwestern Venezuela)

"Big tooth" †*Carcharocles megalodon*

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RESEARCH ARTICLE

Sawfishes and Other Elasmobranch Assemblages from the Mio-Pliocene of the South Caribbean (Urumaco Sequence, Northwestern Venezuela)

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Abstract

The Urumaco stratigraphic sequence, western Venezuela, preserves a variety of paleoenvironments that include terrestrial, riverine, lacustrine and marine facies. A wide range of fossil vertebrates associated with these facies supports the hypothesis of an estuary in that geographic area connected with a hydrographic system that flowed from western Amazonia up to the Proto-Caribbean Sea during the Miocene. Here the elasmobranch assemblages of the middle Miocene to middle Pliocene section of the Urumaco sequence (Socorro, Urumaco and Codore formations) are described. Based on new findings, we document at least 21 taxa of the Lamniformes, Carcharhiniformes, Myliobatiformes and Rajiformes, and describe a new carcharhiniform species (†*Carcharhinus caquetius* sp. nov.). Moreover, the Urumaco Formation has a high number of well-preserved fossil *Pristis* rostra, for which we provide a detailed taxonomic revision, and referral in the context of the global Miocene record of *Pristis* as well as extant species. Using the habitat preference of the living representatives, we hypothesize that the fossil chondrichthyan assemblages from the Urumaco sequence are evidence for marine shallow waters and estuarine habitats.

Introduction

The Caribbean Sea today is environmentally stable and ecologically complex, and it is characterized by high fish diversity [1]. However, the origin of this regional diversity is still somewhat problematic. In particular, Neogene chondrichthyan faunas in the Caribbean region are still little known in comparison with other regions as Europe and North America (e.g. [2]), although several previous works from diverse sedimentary basins exist (e.g. [3–24]) documenting the paleodiversity of Caribbean faunas before and after the complete closure of the Central American Seaway [25].

Alcaldía Bolivariana del Municipio Urumaco and Museo Paleontologico de Urumaco, Estado Falcón, Venezuela. This paleontological collection does not have a website with a public databank. Access to this paleontological collection is permitted for national or foreign researchers with previous permission. Access to the collection is obtained by a request directly with the curator of paleontology collection and the competent authorities of the Bolivarian Mayoralty Urumaco, Falcon State, Venezuela. Other fossils referred and illustrated in our article, belong to the Museo de Ciencias de Caracas (MCNC) and to the Centro de Investigaciones Antropologicas, Arqueologicas y Paleontologicas de la Universidad Experimental Francisco de Miranda, Falcón estate, Venezuela. These institutions have paleontological collections with public access, which is obtained by a request directly with the curator of the collection and the competent authorities. All relevant data necessary to replicate the results presented in our article, are available in these paleontological collections of public access referred above.

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Competing Interests: The authors have declared that no competing interests exist.

During the Miocene, northern Venezuela was close to the gateway between the Atlantic and Pacific Oceans prior to the definitive closure of the Panamanian Isthmus [25], and so faunal changes in this area provide an important perspective on changes in the Caribbean region as a whole. Neogene elasmobranchs from the Miocene of Venezuela have been described previously (e.g., [3, 15, 17, 20, 26]), and here we present new data on the elasmobranchs from the Urumaco sequence of northern Venezuela.

The Urumaco stratigraphic sequence is composed of seven geological units [27], represented by diverse paleoenvironment facies including marine, estuarine, riverine, lacustrine and terrestrial [27, 28]. Throughout the entire section [27], the lithology varies between more terrestrially influenced beds such as coal seams, and marine-influenced facies including sandstones, limestones and shales. The Urumaco sequence exhibits the most diverse vertebrate fauna from the Neogene of the southern Caribbean, including marine, estuarine, and freshwater fishes, freshwater and marine turtles and crocodilians, terrestrial and aquatic/semiaquatic mammals, and birds (e.g., [29– 32]). The stratigraphic sequence and the associated fauna provide unequivocal evidence of a marine coastal/estuarine environment, heavily influenced by a complex hydrographic system that flowed from western Amazonia to the proto-Caribbean Sea during the Miocene (e.g. [27, 31, 33–38]). More than 20 years of paleontological expeditions to the Urumaco region made available the collection of elasmobranch assemblages reported here. We provide a taxonomic revision of the elasmobranch fauna from the Socorro, Urumaco and Codore formations and discuss the paleoenvironmental implications. Importantly, we include new shark and ray occurrence data for Tropical America, and we provide a special detailed taxonomic revision of the specimens of *Pristis* "sawfishes" (Pristidae) found in these assemblages.

Material and Methods

The fossil elasmobranch fauna from the Urumaco sequence presented here consists of 1234 specimens, and comes from 14 localities of the Socorro, Urumaco and Codore formations (Fig 1, S1 Table, S1 and S2 Appendix). Bulk samples of 10 kg each were collected on the outcrop and the sediment was screen washed using 0.5 mm open mesh. The specimens were sorted using a stereomicroscope. Large specimens were surface-collected from the outcrop. The material was collected by the authors and other collaborators since 1993 during several expeditions. The specimens are deposited in the paleontological collections of the Alcaldía Bolivariana de Urumaco (AMU-CURS), Centro de Investigaciones Antropológicas, Arqueológicas, Paleontológicas of the Universidad Experimental Francisco de Miranda (CIAAP, UNEFM-PF), and the Museo de Ciencias de Caracas (MCNC). The systematics for fossil and recent taxa follows Compagno [39] and Cappetta [2], with the exception of the extinct genus *Carcharocles* Jordan and Hannibal [40], whose assignment here has continued the discussion presented by Pimiento et al. [21]; the dental terminology follows Cappetta [2]. Terminology of the internal pristids rostral cavities follows Wueringer et al. [41]. Taxonomic identification included an extensive bibliographical review and comparative studies with fossil and extant specimens from the following collections: Fossil vertebrate section of the Museum für Naturkunde in Berlin (MB), Museo Nacional de Historia Natural de Santiago (SGO-PV) in Chile, Museu Paraense Emilio Goeldi (MPEG-V), Brazil; Natural History Museum of Basel (NMB), Switzerland; Palaeontological Institute and Museum at the University of Zurich (PIMUZ) Switzerland; René Kindlimann (private collection), Switzerland; Smithsonian Tropical Research Institute, Panama (STRI-PPP-T). We gathered habitat information of all taxa with living representatives using Compagno [42, 43], Compagno et al. [44], Musick et al. [45], Voigt and Weber [46], and the FishBase website (http://www.fishbase.org). The S2 Table is based on Aguilera [19], Aguilera and Lundberg [20], Lundberg et al. [47], Aguilera and Marceniuk [48], and Aguilera et al. [31].

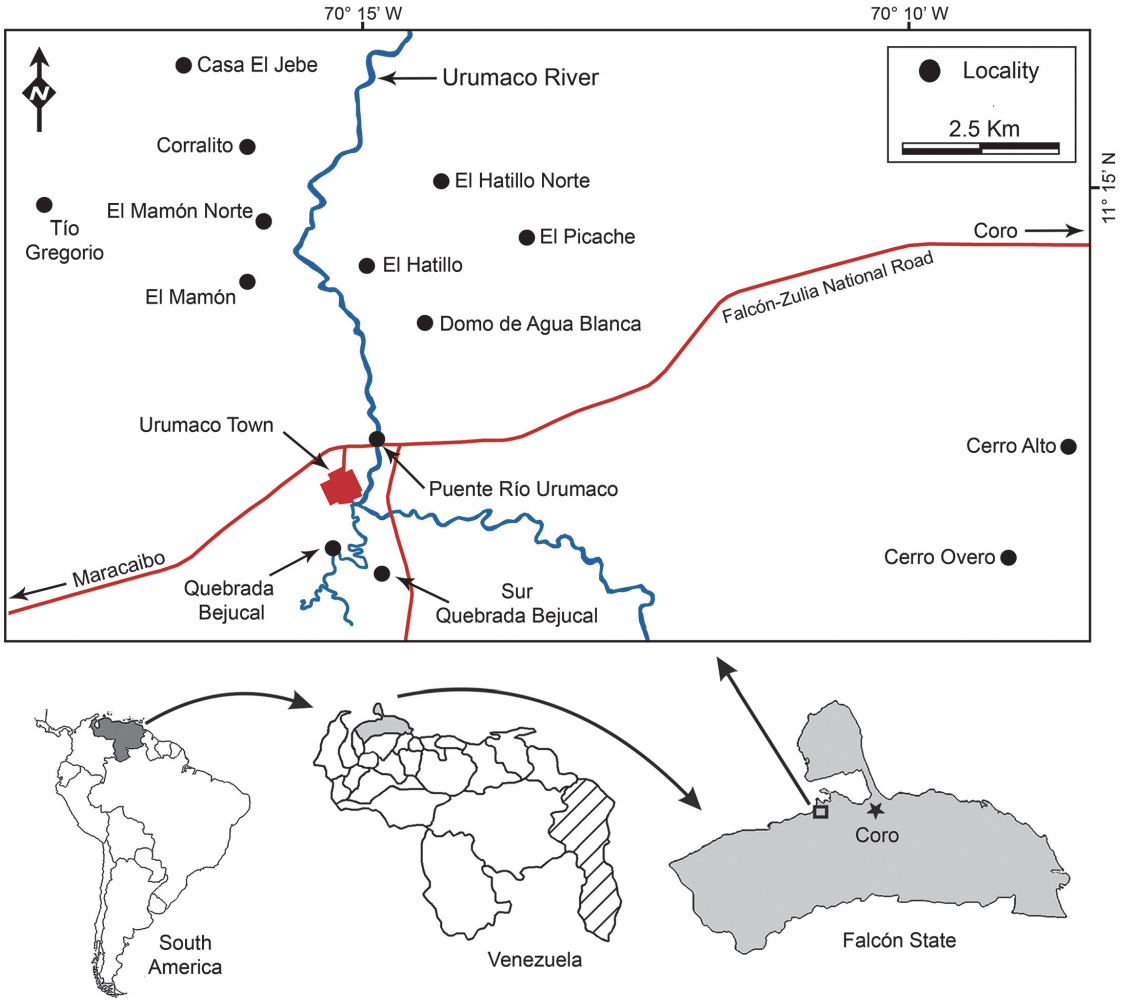

Fig 1. Locality map. Fossiliferous localities of the Urumaco sequence.

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Measurements for *Pristis* rostra follow the recommendations and methods proposed by Whitty et al. [49]. Rostral spine counts for extant species were obtained from the literature, as well as from examination of comparative material housed at the Museum of Natural History Vienna and the Zoological Museum of the University of Zurich. Rostral cavities in the fossil pristids were visible due to pre-existing breaks.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are

available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub: urn:lsid:zoobank.org:pub:8A290D4C-7169-4300-A15C-70942B19D153. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Geological Context

Socorro Formation (Middle Miocene)

The lower and upper contacts of the Socorro Formation (Fig 2) are conformable with the Querales and Urumaco formations, respectively [27, 50, 51]. Hambalek et al. [51] informally divided the Socorro Formation into three members. Later, Quiroz and Jaramillo [27] conducted a detailed sedimentological stratigraphic study, identifying a thickness of 2300 m to the whole Socorro Formation along Paují Creek, 20 km east of the town of Urumaco. The Middle Member is 880 m thick, and is characterized by complex interbedding of medium to fined-grained sandstone, organic mudstone, coal, shales and coquinoidal limestones with abundant mollusks remains [27]. The Upper Member is 639 m thick and it is characterized by gray, massive-bedded, sandy mudstone interbedding with organic mudstones with plants and coal fragments and scarce coquinoidal limestones [27, 51].

Urumaco Formation (middle–late Miocene)

The lower and upper contacts of the Urumaco Formation (Fig 2) are conformable with the Socorro and Codore formations, respectively [27, 51]. The unit has a thickness of approximately 1700–2060 m [27, 50], and toward the east it is correlative with the Caujarao Formation that crops out in the Coro-La Vela region [27, 50]. The unit has been divided in three members: the Lower Member, 780 m thick, is dominated by dark-gray laminated mudstones and shales with interbedding fine-grained sandstone and some coquinoidal limestone layers; the Middle Member is characterized by interbedding of medium-to fine-grained sandstone, organic-rich mudstone, shales and coquinoidal limestones; the Upper Member is composed of laminated organic-rich mudstone and shales intercalated with very fine grained sandstones [27, 50].

Codore Formation (late Miocene–Pliocene)

The lower and upper contacts of the Codore Formation (Fig 2) are conformable with the Upper Member of the Urumaco Formation and the basal conglomeratic level of the San Gregorio formations, respectively [27, 52]. The Codore Formation has been divided into three formal members: El Jebe Member with continental deposits 475 m thick, the Chiguaje Member with marine deposits 65 m thick, and the Algodones Member with continental deposits 320 m thick [27, 52, 53]. The marine Chiguaje Member is characterized by dark-gray laminated mudstones interbedding with fine-grained muddy sandstones and coquinoidal limestones with oysters [27]. Rey [53] assigned an early-late Pliocene age to the Chiguaje Member, based on planktonic foraminifera. Hambalek et al. [51] suggested a late Miocene–Pliocene age for the same member based on palynomorphs, and recently Smith et al. [54] suggested a late Miocene-middle Pliocene age, based on planktonic foraminifera.

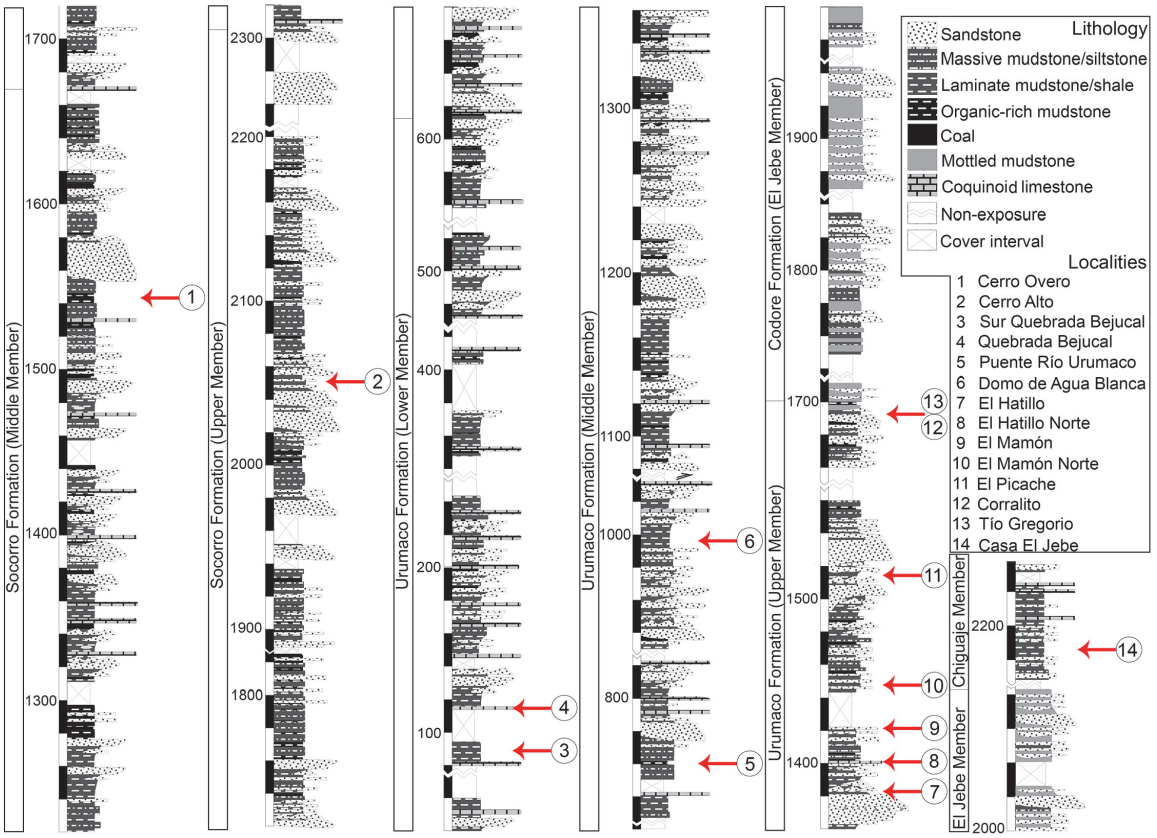

Fig 2. Stratigraphic section of the Socorro, Urumaco and Codore formations. Modified from Quiroz and Jaramillo [27].

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Results

Elasmobranch—systematics

The elasmobranch assemblages from the section of the Urumaco sequence studied here include at least 21 taxa attributed to 13 genera, 9 families and 4 orders (S1 Table).

Neoselachii Compagno, 1977 [55]

Galeomorphii Compagno, 1973 [56]

Lamniformes Berg, 1937 [57]

†Otodontidae Glikman, 1964 [58]

†*Carcharocles* Jordan and Hannibal, 1923 [40]

†*Carcharocles megalodon* (Agassiz, 1843) [59] (Fig 3A–3H)

Description. Fifteen isolated teeth (five upper, seven lower and three of indeterminate jaw position) from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). The crown is triangular in shape, with a flat and convex labial and lingual face, respectively; the lingual face has a typical large neck (inverse "V"-shaped) between

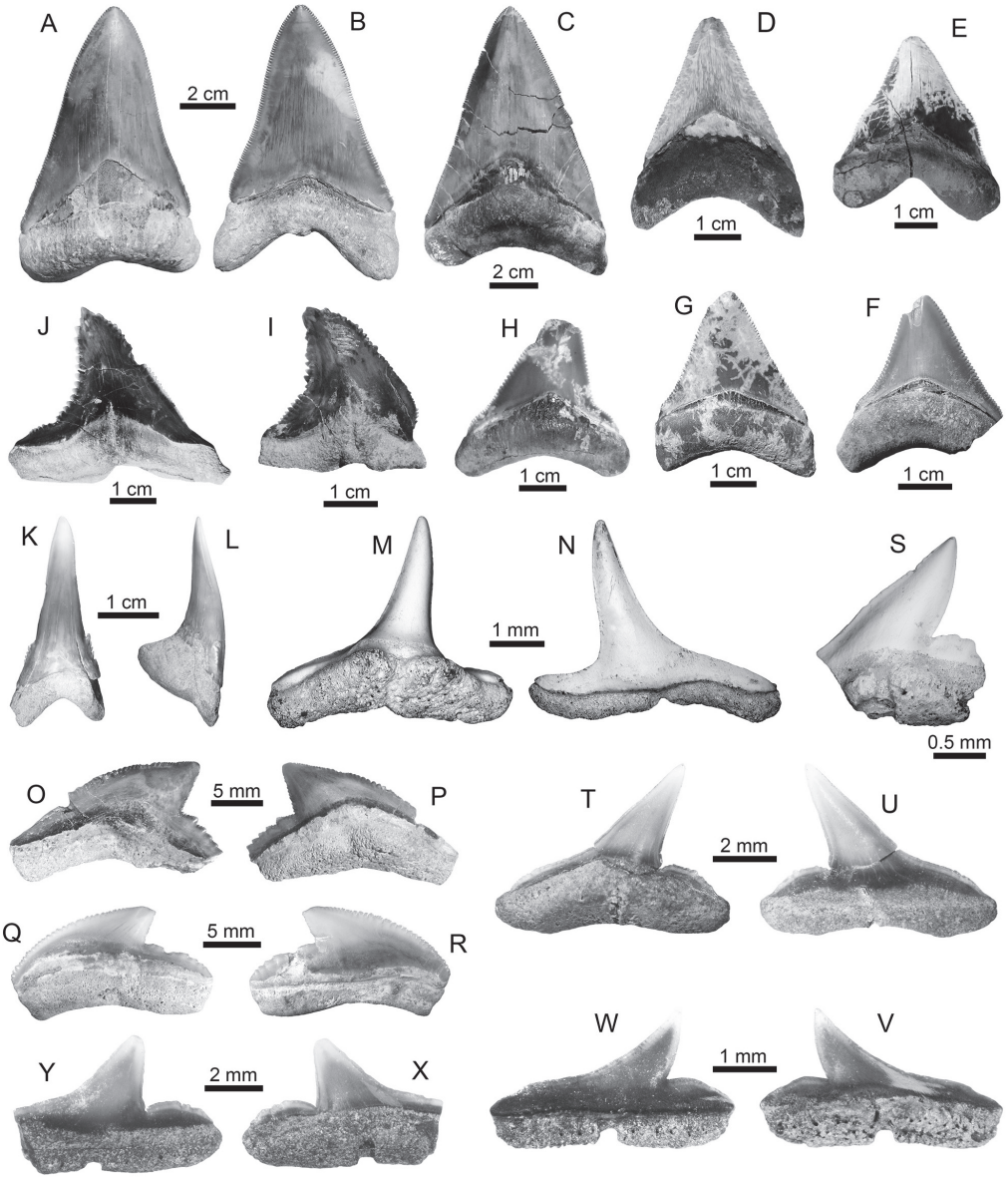

Fig 3. Lamniform and carcharhiniform sharks of the Urumaco sequence. (A-H)

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the crown and the root. Cutting edges are finely serrated. In all teeth, the root is high, its root lobes are well developed and a weak lingual protuberance is present. The teeth range in height from 23 to 99 mm and width from 35 to 69 mm.

†*Carcharocles megalodon*: Urumaco Fm. [A-B: UNEFM-CIAAP-1292, C: AMU-CURS-455, E: UNEFM-PF-388, F-G: AMU-CURS-605, and H: AMU-CURS-338] and Codore Fm. [D: UNEFM-PF-351)]. (**I-L**) †*Hemipristis serra*: Urumaco Fm. [I: AMU-CURS-332, and J: AMU-CURS-331] and Codore Fm. [K-L: AMU-CURS-331]. (**M-N**) *Paragaleus* sp.: Urumaco Fm. [AMU-CURS-640]. (**O-R**) *Galeocerdo cuvier*: Urumaco Fm. [O-P: UNEFM-PF-408] and Codore Fm. [Q-R: AMU-CURS-625]. (**S-Y**) *Rhizoprionodon* sp.: Urumaco Fm. [T-U: AMU-CURS-497, V-W: AMU-CURS-478, and X-Y: AMU-CURS-408] and Codore Fm. [AMU-CURS-635]. View: labial (B, K, N-O, R, U-W, Y), lingual (A-J, M, P-Q, S-T, V, X), profile (L). Abbreviations: Fm., Formation.

Carcharhiniformes Compagno, 1973 [56]

Hemigaleidae Hasse, 1879 [60]

Hemipristis Agassiz, 1835 [59]

†*Hemipristis serra* (Agassiz, 1835) [59] (Fig 3J–3L)

Description. Nineteen isolated teeth (nine upper, eight lower and two of indeterminate jaw position) from the Urumaco (middle–late Miocene) and Codore formations (late Miocene–Pliocene) (S2 Appendix). Upper teeth are labio-lingually compressed, with a triangular crown curved distally. The mesial cutting edge is strongly convex and bears fine serrations that end shortly before reaching the apex; distal edge is concave and coarsely serrated with the serrated part also terminating before reaching the apex. The root is high and compressed, with a strong lingual protuberance. Lower teeth with a long and lingually inclined unserrated crown; there are small cusplets near the crown base and the root is bilobate with a strong lingual protuberance. The teeth range in height from 10 to 47 mm and width from 9 to 46 mm.

Paragaleus Budker, 1935 [61]

Paragaleus sp. (Fig 3M and 3N)

Description. One lower antero-lateral tooth from the Urumaco Formation (middle–late Miocene) (S2 Appendix). The crown is prominent and straight, with smooth concave and convex mesial and distal edges, respectively. The distal heel is shorter than the mesial one, and both are low, smooth, without cusps and slightly recurved to the lingual face. The root is low with a flat base, and the lingual protuberance has a well-defined groove. The tooth height is 4 mm and the width is 4.9 mm.

Remarks. Four extant *Paragaleus* species are known from the Eastern Atlantic and Indo-Pacific regions [44], and two extinct species have been described to the Miocene of Europe [2]. Extant dentitions of *Paragaleus* spp. show strong dignathic and gradient heterodonty; for this reason a single tooth is unlikely to be diagnostic for species. The tooth AMU-CURS-640 resembles the specimen referred to *Paragaleus* sp. by Carrillo-Briceño et al. [62] from the early Pleistocene of Ecuador.

Carcharhinidae Jordan and Evermann, 1896 [63]

Galeocerdo Müller and Henle, 1837 [64]

Galeocerdo cuvier (Perón and Lesueur, 1822) [65] (Fig 3O–3R)

Description. Four isolated teeth with an unknown jaw position, from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). The crown is triangular and curved distally, the labial face is flat and the lingual one is more convex. The mesial cutting edge is convex and slightly sigmoidal with minor serrations; distal cutting edge is shorter and slightly straight with small serrations. The distal heel is long and strongly serrated. The root is low and slightly curved with a weak lingual protuberance. Complete teeth the range in height from 9 to 13 mm, and in width from 15 to 26 mm.

Rhizoprionodon Whitley, 1929 [66]

Rhizoprionodon sp. (Fig 3T–3Y)

Description. Fourteen isolated teeth (four upper, six lower and four of indeterminate jaw position) from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix); most of them are broken and eroded. In upper teeth, the crown is triangular and asymmetric, with a high cusp inclined distally. The mesial cutting edge is slightly concave and the distal cutting edge is slightly straight or sigmoidal; both cutting edges are smooth. The distal heel is high, clearly separated from the cusp by a notch, and this is rounded or finely serrated, depending of the specimen. The root is low with a flat basal face; the labial face is rectilinear and the lingual face has a slight lingual protuberance with a deep medial groove. Complete teeth range in height from 2.5 to 4.4 mm, and in width from 3.5 to 6.3 mm. Due to few diagnostic characters and fragmentary preservation, specimens are not diagnostic to the species level.

Carcharhinus Blainville, 1816 [67]

†*Carcharhinus caquetius* sp. nov. (Fig 4A–4J)

ZooBank life science identifer (LSID) for species. urn:lsid:zoobank.org:act:BE13DF0A-E6F5-44D5-830A-531EE792183D

Etymology. The species is named in honor of the Caquetío pre-hispanic tribe who lived in the Falcon state and other parts of western Venezuela.

Type locality. Puente Río Urumaco, Urumaco Formation (middle–late Miocene), Middle Member, on the right bank of the Urumaco River (near the Urumaco River bridge), northwestern Venezuela (Figs 1 and 2).

Diagnosis. Carcharhinid shark teeth that differ from all other living and extinct *Carcharhinus* species by the following unique combination of dental characteristics: 1) crown with a triangular, strongly elongated and sigmoidal cusp; 2) cusp serrated approximately to its midpoint, with a smooth apex; 3) convex distal heel clearly separated by a deep notch; 4) heel characterized by irregular, small cusps.

Referred material. Holotype: upper lateral tooth (AMU-CURS-499) (Fig 4A–4C); Paratypes: two upper lateral teeth (AMU-CURS-477) (Fig 4D–4F and 4I and 4J), all specimens come from the Middle Member of the Urumaco Formation (Puente Río Urumaco locality).

Description. The teeth range in height from 6 to7 mm and width from 6 to 7.2 mm, including one upper tooth (3406-T-2) from the Angostura Formation (late Miocene), Ecuador (Fig 4G–4H). Teeth are characterized by a triangular shape with an elongate-sigmoidal, narrow and distally deflected cusp. The lingual face is convex and the labial face slightly convex. The mesial cutting edge is slightly convex and sigmoid, without a clear differentiation between it and the mesial heel; the distal edge is concave in the lower part and sigmoid in the upper part. The mesial crown edge has a strong serration that decreases as it approaches the cusp, giving way to a smooth edge at the apex on both edges of the cusp. The distal heel consists of irregular, small cusps, and is well-separated from the distal edge by a deep notch. The root is thick and slightly concave in the base with slightly rounded lobes; the labial surface is flat and the lingual surface has a shallow lingual protuberance with a shallow lingual groove. To date, we have not found any lower tooth with diagnostic features that justify referral to this new taxon.

Remarks. Some extant species of *Carcharhinus*, such as *C. borneensis* (Bleeker, 1859) [68], *C. dussumieri* (Valenciennes, 1839)[69], *C. fitzroyensis* (Whitley, 1943) [70], *C. hemiodon* (Valenciennes, 1839) [69], *C. porosus* (Ranzani, 1839) [71], *C. sealei* (Pietschmann, 1913) [72], *C. signatus* (Poey, 1868) [73], and *C. sorrah* (Valenciennes, 1839) [69], have upper teeth with a generalized morphological pattern characterized by triangular and distally inclined crowns with coarse serration of the distal heel (e.g., [46]). However, diagnostic elements in the morphology of the cups and the regular serration of the distal heel in the extant taxa previously mentioned permit a clear differentiation between these and the upper teeth of *Carcharhinus caquetius* sp. nov., the teeth of which have a diagnostic elongated, sigmoidal cusp, with a

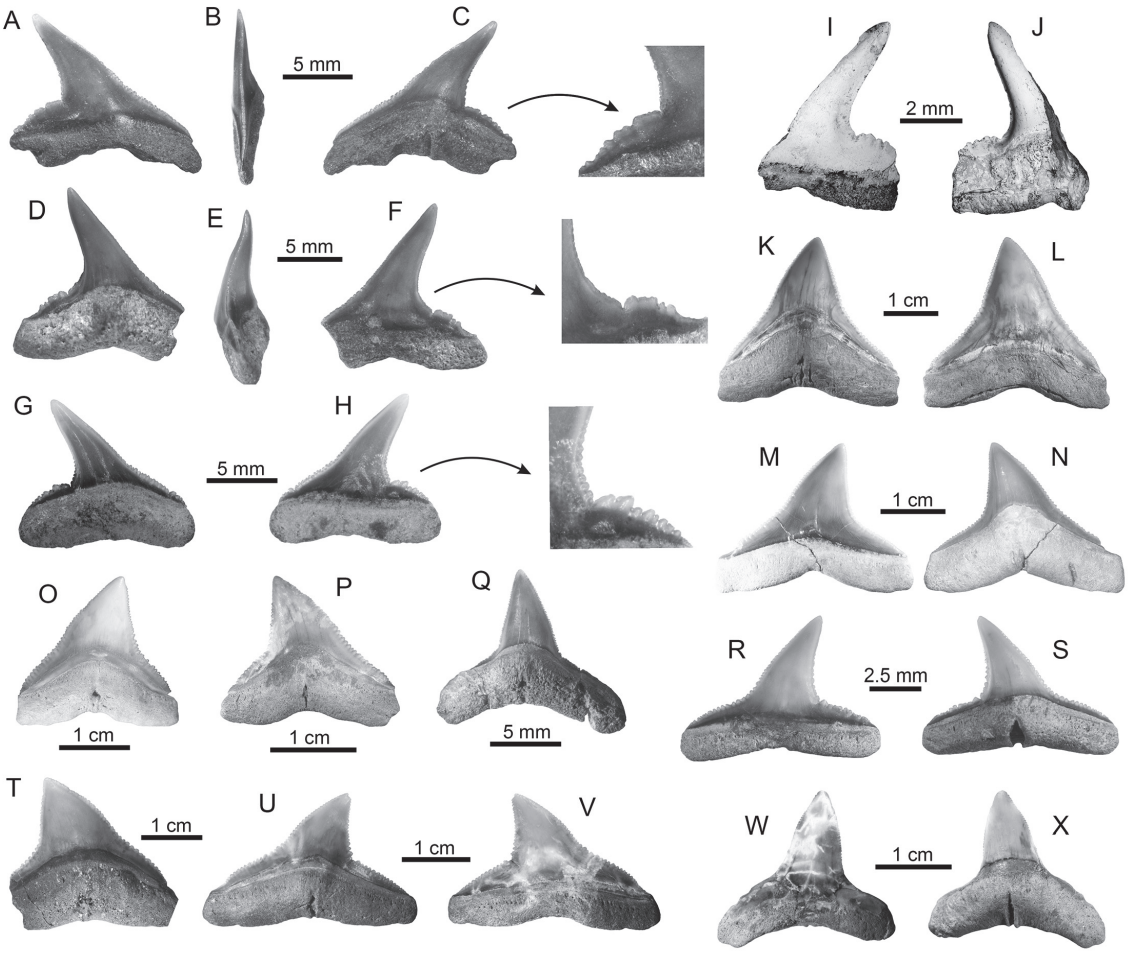

Fig 4. Carcharhiniform sharks of the Urumaco sequence. (**A-J**) †*Carcharhinus caquetius* sp. nov. Holotype: A-C [AMU-CURS-499], paratypes: D-F, I-J [AMU-CURS-477]. (**G-H**) specimen of †*Carcharhinus caquetius* sp. nov. [3406-T-2, 3457-T-(1)] from the Angostura Formation, Ecuador. (**K-Q**) *Carcharhinus leucas*: Urumaco Fm. [K-L: AMU-CURS-360, M-N, Q: AMU-CURS-368], and Codore Fm. [O-P: AMU-CURS-622]. (**R-S**) *Carcharhinus limbatus*: Urumaco Fm. [AMU-CURS-456]. (**T-X**) *Carcharhinus obscurus*: Urumaco Fm. [T: AMU-CURS-464, U-V: AMU-CURS-463, W-X: AMU-CURS-466]. View: labial (A, F, H-I, L-M, R, V-W), lingual (C, D, G, J, K, N-Q, S-U, X), profile (B, E). Abbreviations: Fm., Formation.

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characteristic distal heel conformed by irregular cusps. The extant species most closely related to *C. caquetius* sp. nov. could be *C. signatus*; nevertheless, in the upper teeth of this taxon, such characters as a strong serration in the mesial heel, a strong and regular serration in the distal heel, a flattened labial face, and a smooth or slightly serrated, wider, shorter and straighter cusp, allow differentiation from *C. caquetius* sp. nov. The oldest record of *C. signatus* is from the late Miocene of Panama, where a few specimens have been collected from the Chagres Formation [24]. Some species of *Carcharhinus* have ontogenetic and sexual dental variation [2, 43, 46], which makes the taxonomic determination of isolated teeth difficult, especially when only

few specimens are available. However, the teeth described as *C. caquetius* sp. nov. from the Urumaco Formation, and the specimens from the Angostura Formation (Ecuador), are clearly different from the teeth of other *Carcharhinus* species.

Carcharhinus leucas (Müller and Henle, 1839) [74] (Fig 4K–4Q)

Description. Twenty-eight isolated teeth (twenty upper and eight lower) from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). Upper teeth are characterized by crowns with a triangular shape; the lingual face is convex and the labial one is flat. Cutting edges are regularly serrated; the serrations become progressively coarser near the base of the crown. The mesial cutting edge is straight or slightly convex, and the distal one is slightly concave or straight; the distal heel has a typical serrated blade shape. The root is thick and concave along the basal margin. The labial face of the root is flat and the lingual face is convex and is characterized by a weak lingual groove. Lower teeth have a thick and finely serrated crown with the lateral heel finely serrated; the base of the root is slightly concave. The teeth range in height from 12 to 21 mm and width from 10 to 21 mm.

Carcharhinus limbatus (Müller and Henle, 1839) [74] (Fig 4R and 4S)

Description. Two upper lateral isolated teeth from the Urumaco Formation (middle–late Miocene) (S2 Appendix). The crown is high, triangular and slightly convex with the apex inclined distally. The lingual face is convex and the labial one is flat. The mesial cutting edge is slightly convex and the distal cutting edge concave; both are serrated. The serrations on the mesial and distal heel are more developed and well-differentiated than the cutting edges. The root is wider that the crown and its base slightly concave; the labial face is flat and the lingual protuberance is slightly developed and has a shallow groove. The teeth range in height from 7 to 12 mm and width from 8 to 10 mm.

Carcharhinus obscurus (Lesueur, 1818) [75] (Fig 4T–4X)

Description. Twenty isolated teeth (sixteen upper and four lower) from the Urumaco Formation (middle–late Miocene) (S2 Appendix). Upper teeth are characterized by a triangular shape and lack of an elongate crown with regular serration. The mesial cutting edge is apically convex, with the apex deflected distally; the distal cutting edge is concave. The root is thick, low and slightly concave in the basal margin with slightly rounded lobes; the lingual surface of the root is convex with a shallow lingual groove. Lower teeth have erect crowns finely serrated and moderately arched root lobes. The teeth range in height from 12 to 21 mm and width from 10 to 21 mm.

Carcharhinus plumbeus (Nardo, 1827) [76] (Fig 5A–5F)

Description. Four upper isolated teeth from the Codore Formation (late Miocene–Pliocene) (S2 Appendix). The crown is triangular in shape and strongly elongated with the apex deflected slightly distally; the labial face is flat and the lingual one is convex. The convex mesial crown edge is continuous with the mesial heel. The distal edge is convex or slightly straight and can be differentiated from the distal heel, but a notch is lacking. The cutting edges and heels are uniformly and finely serrated. The root base is slightly concave; the lingual face is convex and it is characterized by a lingual groove. The teeth range in height from 15.5 to 18 mm and width from 7 to 22 mm.

Carcharhinus porosus (Ranzani, 1839) [71] (Fig 5G–5J)

Description. Eight isolated teeth (five upper and three lower) from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). In the upper teeth, the crown is triangular and asymmetric, with a high cusp inclined distally. The mesial edge is straight or lightly concave, and in most of these there is no differentiation between this and the mesial heel; the distal edge is straight. Both cutting edges are strongly serrated, and the serrations decrease in size from the base to the apex. The distal heel is long, strongly serrated and clearly separated from the cusp by a deep notch. The root is low with a slightly concave

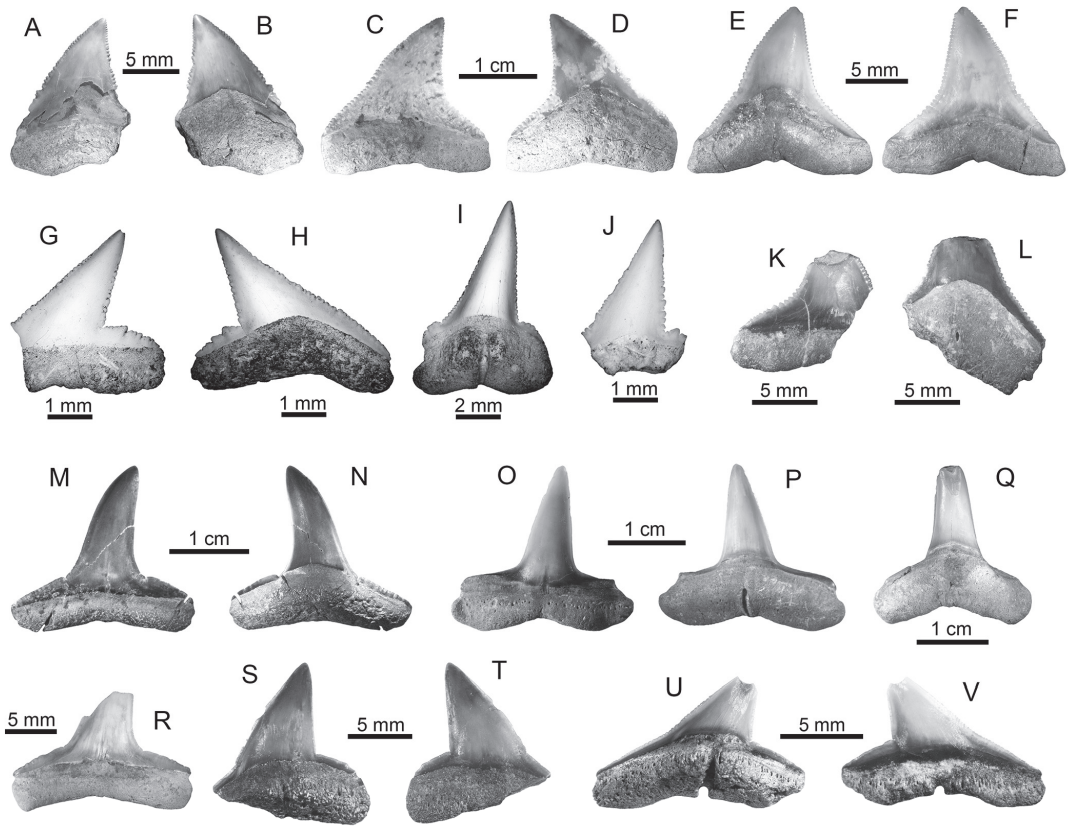

Fig 5. Carcharhiniform sharks of the Urumaco sequence. (**A-F**) *Carcharhinus plumbeus*: Codore Fm. [A-F: AMU-CURS-624]. (**G-J**) *Carcharhinus porosus*: Urumaco Fm. [G-H: AMU-CURS-472, and I: AMU-CURS-590], and Codore Fm. [J: AMU-CURS-631]. (**K-L**) *Carcharhinus* spp.: Socorro Fm. [K-L: AMU-CURS-630]. (**M-R**) *Negaprion brevirostris*: Urumaco Fm. [M-N: AMU-CURS-468, O-P: AMU-CURS-469], and Codore Fm. [Q-R: AMU-CURS-626]. (**S-V**) *Sphyrna* cf. *zygaena*: Urumaco Fm. [AMU-CURS-474; AMU-CURS-477]. View: labial (A, C, F, G, K, M, O, R, T, V), lingual (B, D-E, H-J, L, N, P-Q, S, V). Abbreviations: Fm., Formation.

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base. Lower teeth are incomplete, and show oblique, narrow, serrated cusps with well-differentiated and serrated heels. The teeth range in height from 4.5 to 5 mm and width from 5 to 5.2 mm.

Carcharhinus spp. (Fig 5K and 5L)

Description. Eighty-two incomplete, eroded and non-diagnostic teeth (thirty upper and fifty-two lower) from the Socorro (middle Miocene) and Urumaco (middle–late Miocene) formations (S2 Appendix).

Negaprion brevirostris (Poey, 1868) [73] (Fig 5M–5R)

Description. Twenty-five isolated teeth (fifteen upper and ten lower) from the Socorro (middle Miocene), Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). Upper teeth show a high and triangular cusp slightly inclined distally. The cutting edges are completely smooth, except the low and weakly serrated lateral heels. The root branches are extended and the basal face is rather broad and flat, with a clear medial

lingual groove. Lower teeth are narrower than the upper ones and their heels are generally not serrated. The teeth range in height from 12 to 23 mm and in width from 16 to 22 mm.

Sphyrnidae Gill, 1872 [77]

Sphyrna Rafinesque, 1810 [78]

Sphyrna cf. *zygaena* (Linnaeus, 1758) [79] (Fig 5S–5V)

Description. One upper lateral tooth and one lower lateral tooth from the Urumaco Formation (middle–late Miocene) (S2 Appendix). The upper lateral tooth (height: 12.3 mm) has a high, triangular, asymmetric, broad and distally inclined crown (Fig 5S and 5T); the lingual face is strongly convex and the labial one is flat. The mesial cutting edge is slightly convex and slightly sigmoid and the distal cutting edge is straight; both cutting edges are completely smooth. The distal heel is low and well separated from the cusp by a shallow notch. The root is low with the basal surface slight concave, and is missing the mesial lobe; the lingual protuberance is well developed, bearing a groove. The lower lateral tooth has a stout triangular, slightly serrated crown (Fig 5U and 5V). The lingual face is convex and the labial face is flat. The cusp is inclined distally, being broken and incomplete in the apex. The mesial cutting edge is straight and there is not a clear differentiation between this and the mesial heel; the distal cutting edge is straight. The distal heel is large without serrations and is well separated from the cusp by a shallow notch. The root has a slightly concave base and the lingual protuberance is well developed, bearing a deep groove.

Remarks. Juveniles and young adults of extant *Sphyrna zygaena* have teeth with smooth cutting edges, but larger individuals may have slightly serrated teeth [80, 81].

Batomorphii Cappetta, 1980 [82]

Myliobatiformes Compagno, 1973 [56]

Dasyatidae Jordan, 1888 [83]

cf. *Dasyatis* Rafinesque, 1810 [78] (Fig 6A–6V)

Description. Sixteen isolated teeth of indeterminate jaw position from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). The teeth are small, only a few millimeters wide. The crown shows a middle transverse crest that separates the labial and lingual faces; the crest is lingually elongate and forms a distinctive cusp in male teeth (e.g. Fig 6G–6J, 6U and 6V). The labial face is sub-triangular in shape, with a distinctive alveolate ornamentation, and a labio-lingually extended depression; the lingual face is smooth and is divided into two lingual marginal areas by a lingual ridge. The root has two lobes, which are lingually arched with a flat or slightly bulging base. There is a foramen in the middle of the sulcus.

Remarks. *Dasyatis* shows a dental morphological diversity with distinct gynandric heterodont patterns in most species, which may be more complex at the generic level than currently accepted [2]. Knowledge of dental patterns in extant and fossil *Dasyatis* and others Dasyatidae is still scarce, making any taxonomic assignment of fossil specimens to species difficult.

Dasyatidae indet. (Fig 6W–6X)

Description. One small tooth (less than 2 mm length) with a rhomboid and labial-lingually elongated crown from the Urumaco Formation (middle–late Miocene). The occlusal surface is flat and appears to be eroded; however, this has a light alveolate ornamentation. The root is massive and presents two distinct lobes with a flat basal faces that becomes narrower lingually; between these there is a deep sulcus with two foramina. Due similarities in dental morphology among dasyatid genera and the few fossil specimens referred herein, we maintain this specimen in open nomenclature.

Myliobatidae Bonaparte, 1838 [84]

Aetobatus Blainville, 1816 [67]

Aetobatus cf. *narinari* (Euphrasen, 1790) [85] (Fig 7A–7G)

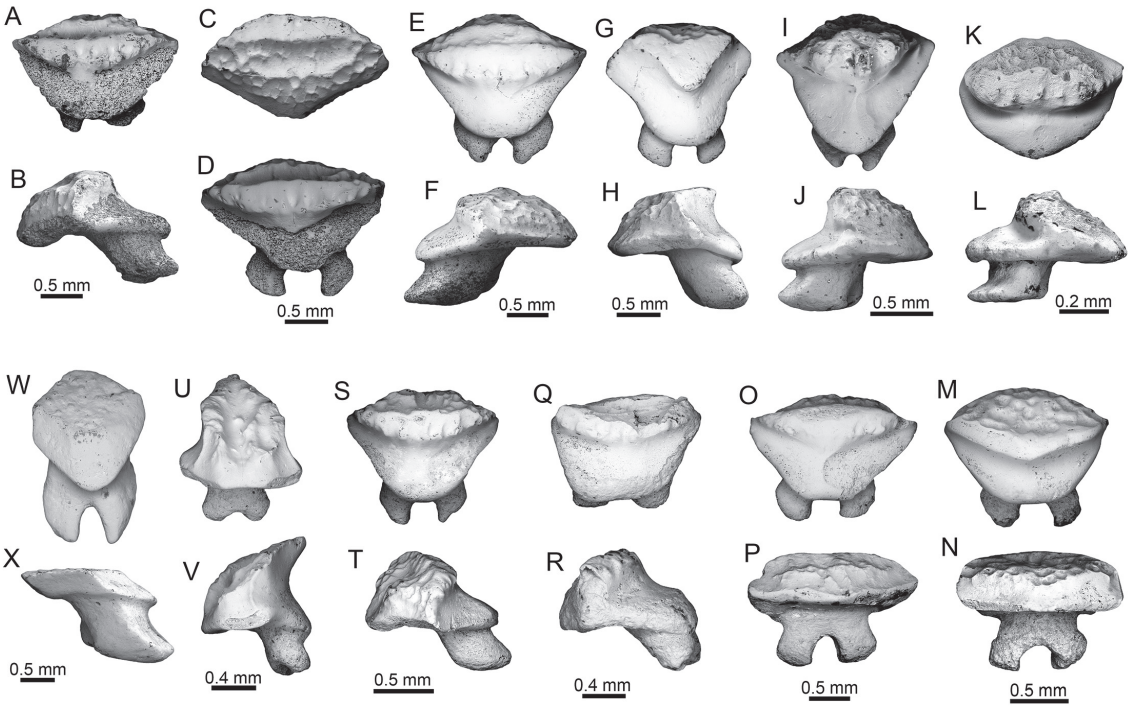

Fig 6. Rays of the Urumaco sequence. (**A-V**) cf. *Dasyatis*: Urumaco Fm. [A-D: AMU-CURS-589, E-F, I-J: AMU-CURS-495, G-H: 496], and Codore Fm. [M-V: AMU-CURS-636]. (**W-X**) Dasyatidae indet.: Urumaco Fm. [AMU-CURS-591]. View: labial (N, P, U), profile (B, F, H, J, L, R, T, V, X), lingual (W), occlusal (A, C-D, E, G, I, K, M, O, Q, S). Abbreviations: Fm., Formation.

doi:10.1371/journal.pone.0139230.g006

Description. Fifty-seven incomplete, isolated teeth (eight upper and forty-nine lower) and two fragmented upper dental plates, from the Socorro (middle Miocene), Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). Upper teeth are almost straight and the lower ones are mesio-distally V-shaped. The crown is labio-lingually thicker in the central than in the lateral region. In occlusal view, the crown surface is smooth and the labial and lingual margins are vertical and strongly ornamented; on the lingual margin there are well marked alternating furrows and laminae, whereas these structures are not so evident on the labial one. The root is polyaulacorhize, apico-basally flattened and decreases in height to the lateral edges of the tooth, and is displaced lingually with respect to the crown.

Remarks. Though the teeth from the Urumaco sequence described here are not adequately preserved, their tooth morphology has strong resemblance to those of the recent species *Aetobatus narinari* [86]. At least two nominal species of *Aetobatus* were described from early to late Miocene deposits of Europe: *Aetobatus arcuatus* (Agassiz, 1843) [59] and *Aetobatus cappettai* Antunes & Balbino, 2006 [87]. *Aetobatus arcuatus* is possibly restricted to the early-middle Miocene, and *A. cappettai* has only been reported from the late Miocene of Portugal [88]. For a recent discussion of Miocene *Aetobatus* teeth, see Bor et al. [89].

Myliobatis Cuvier, 1816 [90]

Myliobatis sp. (Fig 7H–7J)

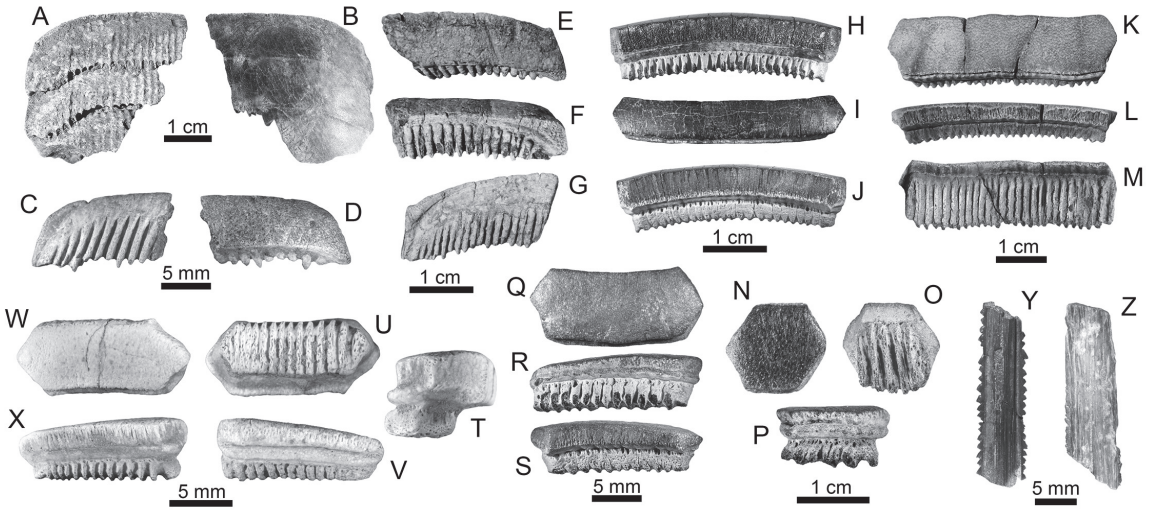

Fig 7. Rays of the Urumaco sequence. (**A-G**) *Aetobatus* cf. *narinari*: Urumaco Fm. [E-G: AMU-CURS-308] and Codore Fm. [A-B: AMU-CURS-598, and C-D: AMU-CURS-614]. (**H-J**) *Myliobatis* sp.: Urumaco Fm. [AMU-CURS-487]. (**K-X**) *Rhinoptera* sp.: Urumaco Fm. [K-P: AMU-CURS-288, and Q-S: AMU-CURS-489], and Codore Fm. [T-X: AMU-CURS-621]. (**Y-Z**) Myliobatiformes indet.: Urumaco Fm. [Y: AMU-CURS-492], and Codore Fm. [Z: AMU-CURS-634]. View: basal (A, C, G, M, O, U), dorsal (Z), labial (J, L, S, X), profile (T), lingual (F, H, P, R, V), occlusal (B, D-E, I, K, N, Q,), oblique occlusal (W), ventral (Y). Abbreviations: Fm., Formation.

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Description. With 798 teeth (indeterminate upper-lower jaw position), this is the most abundant taxon sampled from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). The specimens consist of complete and fragmented isolated teeth, mainly from the medial (780 specimens) and lateral tooth row (18 specimens). The medial teeth are broader (mesio-distally) than long (labio-lingually), with a hexagonal contour, and in most cases are rectilinear, but some are arched. Teeth of lateral and posterior files are longer than broad, with a hexagonal, pentagonal or triangular contour depending on their position in the files. In all teeth, the occlusal crown face is practically flat and the labial and lingual margins are slightly ornamented; the root has a polyaulacorhize vascularization type. Complete teeth range in width from 8 to 57 mm, and height from 3 to 10 mm.

Remarks. Taxonomic identification based on isolated teeth of *Myliobatis* is difficult due to the large dental variation within the group [86, 91].

Rhinopteridae Jordan and Evermann, 1896 [63]

Rhinoptera Cuvier, 1829 [92]

Rhinoptera sp. (Fig 7K–7X)

Description. Fifty complete and incomplete isolated teeth (14 mesial and 36 laterals of indeterminate upper-lower jaw position) recovered from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). The crown is variably high, hexagonal, straight or slightly convex labially. The occlusal surface is flat and there is a thick basal ledge on the lingual face of the crown. Lateral teeth are less enlarged than the medial ones, showing a regular hexagonal shape; the distal crown height is typically lower than mesial height. The root has polyaulacorhize vascularization type, with a quadrangular shape, and does not project beyond the level of the crown. Complete teeth range in width from 13 to 38 mm, and height from 3 to 9 mm.

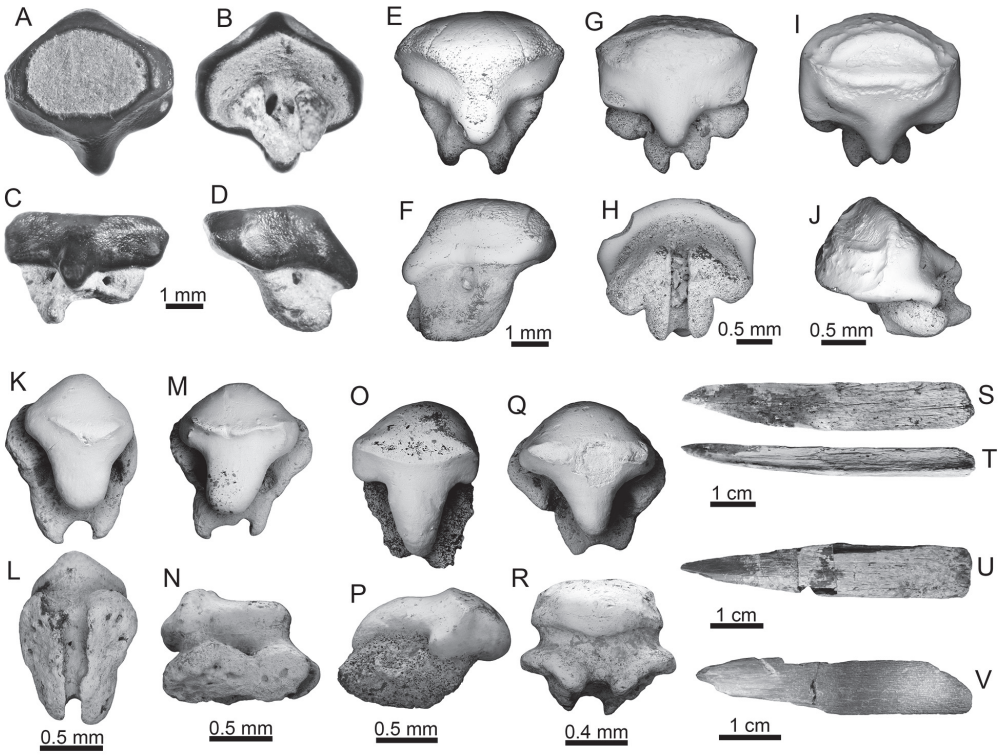

Fig 8. Guitarfish and sawfish of the Urumaco sequence. (**A-J**) *Rhynchobatus* spp.: Urumaco Fm. [A-D: AMU-CURS-482 and E-F: AMU-CURS-628], Codore Fm. [G-J: AMU-CURS-638]. (**K-V**) *Pristis* sp. Buccal teeth: Urumaco Fm. [K-R: AMU-CURS-484], and rostral spines: Urumaco Fm. [S-T: AMU-CURS-243 and U: AMU-CURS-244], and Codore Fm. [V: AMU-CURS-620]. View: basal (B, H, L), dorsal (S), labial (R), profile (D, F, J, N, P), lingual (C,), occlusal (A, I, K, M, O, Q), oblique occlusal (E, G), ventral (U-V), posterior (T). Abbreviations: Fm., Formation.

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Remarks. As in *Myliobatis*, the taxonomic identification of isolated teeth of *Rhinoptera* is extremely difficult due to extensive dental variation in the group (e.g., [86]).

Myliobatiformes indet. (Fig 7Y and 7Z)

Description. Six fragmented caudal spines from the Urumaco (middle–late Miocene) and Codore (late Miocene–Pliocene) formations (S2 Appendix). The specimens preserved an evident dorsal groove, a ventral central ridge and strong serrations along both sides of the spine.

Remarks. The majority of myliobatiforms have caudal spines and some characters can be used to identify fossil taxa [86]; however due the fragmentary condition of the specimens referred herein, these characters cannot be usually observed.

Rajiformes Berg 1937 [57]

Rhynchobatidae Garman, 1913 [93]

Rhynchobatus Müller and Henle 1837 [64]

Rhynchobatus spp. (Fig 8A–8J)

Description. Three isolated teeth of indeterminate jaw position from the Urumaco Formation (middle–late Miocene), and two from the Codore Formation (late Miocene–Pliocene) (S2 Appendix). Teeth from the Urumaco Formation have a globular and lozenge-shaped

crown with rounded edges and with a fine granular ornamentation. The labial face is strongly convex and the lingual face presents an uvula that extends beyond the root sulcus. The uvula is flanked on both sides by a slight depression. The occlusal part of the crown in one of the specimens is flattened due to wear (Fig 8A–8D). The root is massive and presents two distinct lobes with a flat basal face that becomes narrower lingually; between these there is a root sulcus with two foramina. The teeth range in width is from 4.9 to 5 mm, and height from 4.7 to 5 mm. The two specimens from the Codore Formation have a globular and lozenge-shaped crown with rounded edges. The labial face is strongly convex and the lingual face presents an uvula that extends beyond the root sulcus. Both specimens have a very prominent arched transverse keel on the crown. The specimen AMU-CURS-638-a (Fig 8I and 8J) shows ridges and a broad, shallow depression on the labial face of the crown. The root is massive and presents two distinct lobes with flat basal faces that become narrower lingually; between these there is a root sulcus with two foramina. The teeth range in width from 2 to 2.1 mm, and height ranges from 1.9 to 2 mm.

Remarks. The specimen AMU-CURS-477-a has morphology similar to an isolated tooth from the late Miocene of Panama referred to *Rhynchobatus* sp. by Pimiento et al. [23]. Because of the range of dental variation in extant species is unknown, and recovered specimens are rare and poor preserved, we refrain from taxonomic identification at species level.

Taxonomic and morphological features of sawfish material in the sequence

The sawfish specimens (Pristidae Bonaparte, 1838 [84]) are represented by two partial rostra from the Socorro Formation (middle Miocene); four buccal teeth, one complete rostrum, 21 partial rostra, 42 rostral spines from de Urumaco Formation (middle–late Miocene), and one rostral spine from the Codore Formation (late Miocene–Pliocene) (S2 Appendix). We examined multiple morphological features, including buccal teeth (Fig 8K–8R), rostral spine shape (Fig 8S–8V), alveolar shape, and the ratio between the total rostral length and the standard rostral length. All specimens recovered from the Miocene of the Urumaco sequence are referable to *Pristis* Linck, 1790 [94] (Figs 8K–8R, 8S–8V and 9A–9L) rather than to *Anoxypristis* White and Moy-Thomas, 1940 [95], based on the internal morphology of the rostrum, as well as the shape of the spines [41]. The most complete specimen from the Urumaco sequence is AMU-CURS-023 (Urumaco Formation, Lower Member) (Fig 9A), previously referred by Aguilera [19] to the extant species *Pristis pectinata* Latham, 1794 [96]. Based on our study of numerous aspects of morphology, the pristids from the Urumaco sequence fall within the rostral morphospace of modern *Pristis* species, however are not easily referable to any one fossil or extant species.

Buccal tooth morphology. The four buccal teeth of indeterminate jaw position (Urumaco Formation, Middle Member) (Fig 8K–8R) are less than 1 mm long. The crown is semiglobular and rounded, with a transverse crest and a long uvula that does not extend beyond the root. The root is much broader than the crown; the furrow is broad and has a large foramen. Oral teeth are somewhat difficult to identify because those of extant species are poorly known and are morphologically variable [2]. According to Cappetta [2], teeth of *Pristis pristis* (Linnaeus, 1758) [79], are longer than broad; however, the teeth of *Pristis pectinata* illustrated by Herman et al. [97], show variability in length and shapes. The specimen from the Urumaco Formation also differs from the buccal teeth of *Pristis aquitanicus* Delfortrie, 1872 [98], described from the early-middle Miocene of France, and illustrated by Cappetta [99].

Rostral spine morphology. Although often referred to as teeth, the rostral spines are not homologous with the buccal teeth of other vertebrates and represent an independent derivation

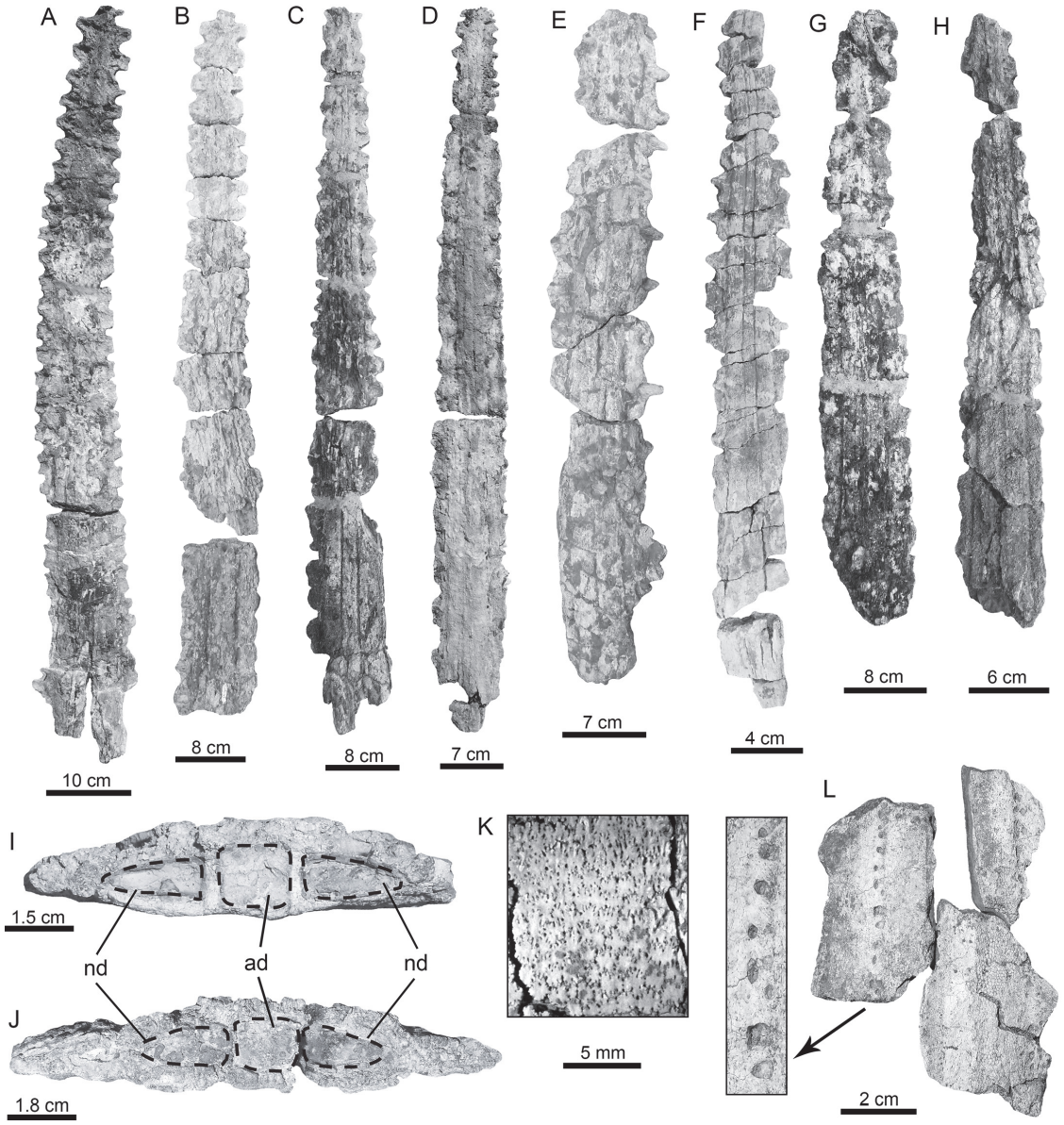

Fig 9. Sawfish rostra of the Urumaco sequence. (**A-L**) *Pristis* sp. rostra: Socorro Fm. [E: AMU-CURS-639 and F: AMU-CURS-241] and Urumaco Fm. [A: AMU-CURS-023, B: AMU-CURS-043, C: AMU-CURS-235, D: AMU-CURS-237, G: AMU-CURS-236, H: AMU-CURS-238 and L: AMU-CURS-251]. (**I-J**) transverse section: [I: AMU-CURS-043 and AMU-CURS-376, Urumaco Fm.]. (**K**) mineralized cartilage: [AMU-CURS-235]. (**L**) fragment of rostrum showing the depressions and foramina interpreted as ampullae of Lorenzini. View: dorsal (A-H), posterior (I-J). Abbreviations: Fm., Formation; ad, axial duct; nd: neural ducts.

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Table 1. Measurements and ratios for extant *Pristis* spp. and rostra from the Urumaco sequence.

	Rostral spine count	SRL	SRW (TW)	DS	DPS	SRW/SRL	TW/SRL	SRL/TRL
Anoxypristis	16–33			1.1–2.0	0.16–0.44	0.08–0.15	0.05–0.08	0.59–0.81
P. pristis	14–24			2.0–2.9	0.53–1.05	0.15–0.25	0.06–0.1	0.91–0.98
P. clavata	18–27			1.2–2.0	0.25–0.7	0.16–0.22	0.07–0.11	0.89–0.97
P. zijsron	23–37			1.1–2.0	0.1–0.33	0.09–0.17	0.04–0.09	0.85–0.97
P. pectinata	20–30			2.1	0.21–0.41	0.13–0.15	0.07–0.08	0.86–0.99
P. atlanticus†	~20	116.3	14.5 (7.0)	—	0.29	0.12	0.06	—
AMU-CURS-023	23/24	70.9	10.7 (5.5)	2.0	0.57	0.15	0.08	0.88
AMU-CURS-235	23	57.7	7.6* (3.4)	—	0.25	0.13	0.06	—
AMU-CURS-237	20+	75.0	8.1 (4.5)	1.65	0.52	0.11	0.06	—

Data from Whitty et al. [49], except *P. pectinata* ratios which are from 14 individuals listed in Robillard and Séret [116], and *P. atlanticus* (rostral spine estimate from Casier [108]; measurement data from Zbyszewski [117]).

*Estimate based on doubling the width of the preserved half.

DS = sum of the distal and next most distal interalveolar ratios from the right and left sides; DPS score = ratio between the spacing of the most anterior two and most posterior two rostral spines; SRL = standard rostral length; SRW = standard rostral width; TRL = total rostral length; TW = tip width

† = extinct taxon.

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from highly modified scales [100]. Isolated rostral spines (Fig 8S–8V) have a length up to 95 mm; these are generally long, pointed and slightly curved distally. The anterior edge is sharp and the posterior edge is concave. These rostral spines are rarely preserved in association with rostra from the Urumaco sequence. An exception to this is the specimen AMU-CURS-251 (Urumaco Fm., Upper Member), which preserves a single associated spine, and AMU-CURS-237 and AMU-CURS-639 (Socorro Formation, Upper Member), in which multiple spines are preserved, but are heavily damaged and all lack distal tips. The spines of AMU-CURS-639 are robust, and both the rostral spines of this specimen and the isolated rostral spine of AMU-CURS-376 have a rounded anterior margin and a grooved posterior margin. These features are consistent with *Pristis*, as noted by Cappetta [2] and inconsistent with *Anoxypristis*. Alveoli are anteroposteriorly asymmetrical, with convex anterior edges and weakly concave posterior edges.

Rostral spine count. An accurate rostral spine count was available only for the rostrum AMU-CURS-023 (Fig 9A). In this specimen, 24 alveoli were found on the right-hand side of the rostrum, and 23 on the left. This count is notably lower than the count of 26 recorded by Aguilera [19] for the same specimen. Counts of 23 and 24 are consistent with every extant pristid [49, 101] (Table 1) although at the lower limit of the range for *Pristis zijsron* Bleeker, 1851 [102], and the high end of the range of *P. pristis*. Rostral spine counts appear to vary on a regional basis in pristids, and the Recent Western Atlantic population of *P. pristis* has a lower count than other populations. In contrast, the Western Atlantic population of *P. pectinata* has a higher count [103]. The specimen AMU-CURS-043 (Urumaco Formation, no collections data about member) (Fig 9B), although incomplete posteriorly and with erosion of the posterior penultimate segment preventing any count from this certainly spine-bearing region, shows a count of 22 alveoli on the best preserved side. The specimens AMU-CURS-235 and AMU-CURS-237 (both from the Urumaco Fm., Upper Member) (Fig 9C and 9D), although less well-preserved than AMU-CURS-023 and with some uncertainty regarding posterior completeness, have minimum counts of 23 and 20 alveoli on the right side, respectively (best preserved side).

Internal duct morphology. Several of the *Pristis* rostra from the Urumaco sequence preserve the internal rostral cavities, often filled with sedimentary material that increases contrast

with the rostral cartilages (Fig 9I and 9J). Anteriorly, only the ducts for the ophthalmic and buccal nerves (following Wueringer et al. [41]) are present; the precranial cavity is absent. The neural ducts are roughly ovate, tapering slightly laterally. Posterior to this, the precranial cavity first appears as a dorsal and a ventral opening. Preservation does not permit assessment as to whether these are connected by a medial constriction, or separated by mineralized cartilage (AMU-CURS-241 and AMU-CURS-376); however slightly more posteriorly they are joined by a medial constriction, and the dorsal and ventral portions are expanded parallel to the rostral margins (AMU-CURS-376) (Fig 9J). The precranial cavity becomes square in outline, and increases in size. The neural ducts develop flattened medial edges, and more tapered lateral edges. The dorsal surface of the axial duct is embayed to contain a small foramen located dorsal to the precranial cavity. This secondary duct in the precranial cavity is found in all adequately preserved rostra from the Socorro and Urumaco formations, and has also been figured in some extant *Pristis* material (e.g. [104]). Its presence has been explained as an artifact relating to shrinking of the hyaline cartilage during the preparation of dried specimens [105], and a similar explanation cannot be ruled out in the fossil material. The structure of the internal rostral cavities is broadly similar to those described and illustrated for *Pristis* by Duméril [104], Hoffmann [105], Kirkland and Aguillón-Martínez [106], Cicimurri [107], and Wueringer et al. [41]. The presence of a single, oval to tear-drop shaped neural duct as opposed to two circular ducts differentiates the genera *Pristis* and *Anoxypristis* [41].

Mineralized cartilage organization. The *Pristis* rostra from Socorro and Urumaco formations share a complex pattern of rostral mineralization. There are two thick layers of prismatic calcified cartilage surrounding the external surface of the rostrum, forming embayments for the alveoli and surrounding the neural canals. On the inner surface of the neural canals, a third layer is present, thinner than the two thus described and not as clearly composed of discrete prisms. There also appears to be an additional, very thin layer of mineralized tissue on the external surface of the rostrum. As many of the rostra are quite weathered, this feature can be seen in only a few specimens. It has a fibrous appearance in macroscopic view. Recent sawfish rostra have been described as consisting of three mineralized cartilage layers [105, 108]: an external prismatic layer and prismatic layers encircling the neural ducts, and a layer lining the neural ducts. Hoffmann [105] mentioned the fibrous outer layer of connective tissue, but did not suggest that it was normally mineralized; however this outer mineralized layer was preserved in *Pristis propinquidens* Casier, 1949 [108]. Many authors failed to note the mineralized layer lining the neural ducts [41, 106], but the studies of Hoffmann [105] and Casier [108], demonstrated that this mineralized layer is present in both Recent and fossil *Pristis* species.

Ampullae of Lorenzini. Depressions and foramina are visible in the mineralized fibrous layer on the ventral surface and immediately lateral to the neural duct of one of the more exceptionally preserved rostra AMU-CURS-251 (Fig 9L). These are distributed in approximately two closely spaced rows parallel to the edge of the neural duct, and are interpreted as housing the ampullae of Lorenzini, with the foramina transmitting the sensory nerves from the lateral line and ampullae of Lorenzini. These depressions were interpreted as related to electroreception rather than to the lateral line system, as the latter, while occasionally associated with subdermal tissues [109] is described as being composed of tubules rather than clusters of receptors. In contrast, the ampullary clusters are not part of a continuous tubular system and are described specifically as being embedded in connective tissue [110]. Differences exist in the distribution pattern of the ampullae of Lorenzini between *Anoxypristis*, *Pristis pristis* and *P. clavata* Garman, 1906 [111] (e.g. [110]). There is no information available as to whether the distribution of ampullae in the intact rostrum mirrors the pattern of fossae in the fibrous outer mineralized layer of the ventral surface of the rostrum. Assuming that it does, the distribution

of ampullae seen in the *Pristis* material from the Socorro and Urumaco formations is closer to that of smalltooth sawfish (*P. zijsron*, *P. pectinata*, and *P. clavata*) than to *P. pristis*.

Discussion

Taxonomic composition

The elasmobranch faunal assemblages described here from the Urumaco sequence include at least 21 taxa (S1 Table), of which only three are extinct (*Carcharocles megalodon*, *Hemipristis serra* and *Carcharhinus caquetius* sp. nov.). From the complete assemblages, two taxa were found to be new fossil records for Venezuela and the Caribbean region (*Carcharhinus caquetius* sp. nov., and *Carcharhinus porosus*). The remaining taxa have been recorded from other Neogene marine deposits of Venezuela [20], Central, North, and South America [18, 24, 62]. Many of the taxa from the Urumaco sequence have also been found in Neogene rocks around the world [2], confirming the cosmopolitan distribution of many of these species during the Miocene–Pliocene.

The elasmobranch fauna of the Urumaco sequence shows a clear differentiation in paleodiversity between geologic units. The Urumaco Formation, with 11 localities, has a paleodiversity of 20 taxa, while the Codore Formation, with only one studied locality, is characterized by 16 taxa and the Socorro Formation only by six taxa (S1 Table). The low paleodiversity of the Socorro Formation in comparison with the other units could be attributable to less intensive sampling. In spite of their absence from the Urumaco sequence, taxa such as *Carcharocles megalodon* and *H. serra* have been found in the Socorro Formation at outcrops located closer to Coro City [3].

Fossil taxa such as *Galeocerdo cuvier*, *Rhizoprionodon* sp, *Carcharhinus leucas*, *C. limbatus*, *C. obscurus*, *C. plumbeus*, *C. porosus*, *Negaprion brevirostris*, *Sphyrna* cf. *zygaena*, *Sphyrna* sp., cf. *Dasyatis*, *Aetobatus* cf. *narinari*, *Myliobatis* sp., *Rhinoptera* sp., and *Pristis* sp. have extant counterparts in tropical America and adjacent regions; other taxa such as the genus *Rhynchobatus* live exclusively in the eastern Atlantic (off the African coast) and Indo-West Pacific [112]. The occurrence of *Rhynchobatus* in the marine facies of the Urumaco and Codore formations and in other geologic units of Venezuela [20], Costa Rica [10], and Panamá [23] confirms the presence of this taxon in the Caribbean region during the late Miocene, suggesting that it became extinct from the proto-Caribbean Sea and western Atlantic, possibly as a consequence of environmental changes during the final stage of closure of the Panamanian isthmus [25], or due to competition with other species. The presence of *Carcharhinus caquetius* sp. nov. in the late Miocene of Ecuador suggests a neritic distribution in the proto-Caribbean and Eastern Pacific for this species.

Taxonomic and morphological features of sawfish

There are four valid extant species of *Pristis*, *P. pristis*, *P. clavata*, *P. zijsron* and *P. pectinata*, supported by morphological and molecular data [103]. *P. pristis*, with a circumtropical distribution, is the sister taxon to the others ("smalltooth sawfish"), all of which show more localized distributions either in the Atlantic-Caribbean (*P. pectinata*) or the Indo-West Pacific (other species). The number and spacing of rostral spines has some discriminatory power in identifying the extant species of *Pristis*, although extensive variation within and between populations has been noted [101, 103]. The number of spine positions is determined early in embryological development [113], however, the environmental and developmental factors underlying the number and position of the rostral spines are unknown.

Whether all *Pristis* material from the Urumaco sequence can be referred to a single species must be considered. This question is especially relevant since modern sawfish species have

overlapping geographic ranges [101], and in historic times, the living species *P. pristis* and *P. pectinata* were present sympatrically in the Caribbean and Gulf of Mexico [114, 115]. At present, there seems to be little evidence for two fossil species in the Urumaco Formation, although the range of DPS values is quite broad (Table 1), especially including the specimen AMU-CURS-235. However, based on other metrics this specimen is generally consistent with other material from the locality, and due to poor preservation on the posterior right side, it is possible that rostral spine spacing is anomalous on the left and is giving a false signal.

Based on our study of numerous aspects of morphology, the Miocene pristids from the Urumaco sequence fall within the rostral morphospace of modern *Pristis* spp., nevertheless, are not easily referable to any one extant species. The *Pristis* material from the Urumaco sequence shows overlap in the number of rostral teeth with *P. pristis*, although at the upper end of the range of this species. Nonetheless, if the whole Venezuelan collection is considered as a single species, DS and DPS values lie outside of the recorded range of *P. pristis* (Table 1). In addition, the posterior rostrum is more slender (SRW/SRL), and the space between the most posterior rostral spine and the chondrocranium is greater (TRL/SRL). In general, the combination of these variables suggests that the fossil material of sawfish from the Urumaco sequence is inconsistent with *P. pristis*, and should be included within the smalltooth sawfish clade.

Within the smalltooth sawfishes, *P. clavata* has a more robust rostrum with a shorter space anterior to the chondrocranium than the Urumaco sequence material (Table 1). Generally high DPS scores and lower rostral spine counts also make referral to *P. zijsron* unlikely. While geographic distribution is most consistent with *P. pectinata*, the high DPS score and slightly narrower rostra of the best-preserved Urumaco material creates uncertainty. *P. zijsron* and *P. pectinata* are sister taxa [103], and there may have been less differentiation in rostral morphospace occupation in Miocene smalltooth sawfish of this lineage, including the Urumaco rostra and *P. atlanticus* from the middle Miocene of Portugal [117].

The total rostral length in *Pristis* is generally considered to be between 1/3 and 1/5 of the total length of the fish [118], and provides a broad size estimate of between 2.4–4 m total length for AMU-CURS-023, 2.1–3.5 m total length for AMU-CURS-235, and 2.7–4.8 m total length (AMU-CURS-237). *P. pectinata* is thought to reach maturity at 2.7–3.6 m, and has a maximum length of over 6.0 m [119]. It seems likely that AMU-CURS-023 and AMU-CURS-237 are adults, and AMU-CURS-235 is either a large juvenile or small adult, but that all are within the size range predicted by extant *Pristis* species, and specifically *P. pectinata*.

Paleoenvironment and paleoecology

The elasmobranch faunistic assemblages from the Urumaco sequence (S1 Table) are distributed across a section more than 2800 m thick (Fig 2). The marine facies in the three members of the Urumaco Formation and in the Chiguaje Member (Codore Formation) have been characterized by Smith et al. [54] as shallow water paleoenviroments based on the study of foraminifera. In addition, most of the living elasmobranch taxa closely related to taxa from the Urumaco sequence prefer coastal habitats, with the exception of some species that show broader preferences (Fig 10). Extant taxa such as *Galeocerdo cuvier*, *Carcharhinus leucas*, *C. limbatus*, *C. obscurus*. *C. plumbeus*, *C. porosus*, *Negaprion brevirostris*, *Sphyrna zygaena*, *Aetobatus narinari* and representatives of the genera *Paragaleus*, *Rhizoprionodon*, *Dasyatis*, *Myliobatis*, *Rhinoptera*, *Rhynchobatus*, and *Pristis* are common inhabitants of marginal marine environments [39, 44–46]. Using the habitat preferences of living elasmobranchs (Fig 10), paleoenvironments suggested in previous studies [27], and the wide range of fossils vertebrates such as reptiles (crocodiles and turtles), mammals (cetaceans and sea cows), and especially bony fishes (S2 Table), that have been described from the whole stratigraphic sequence

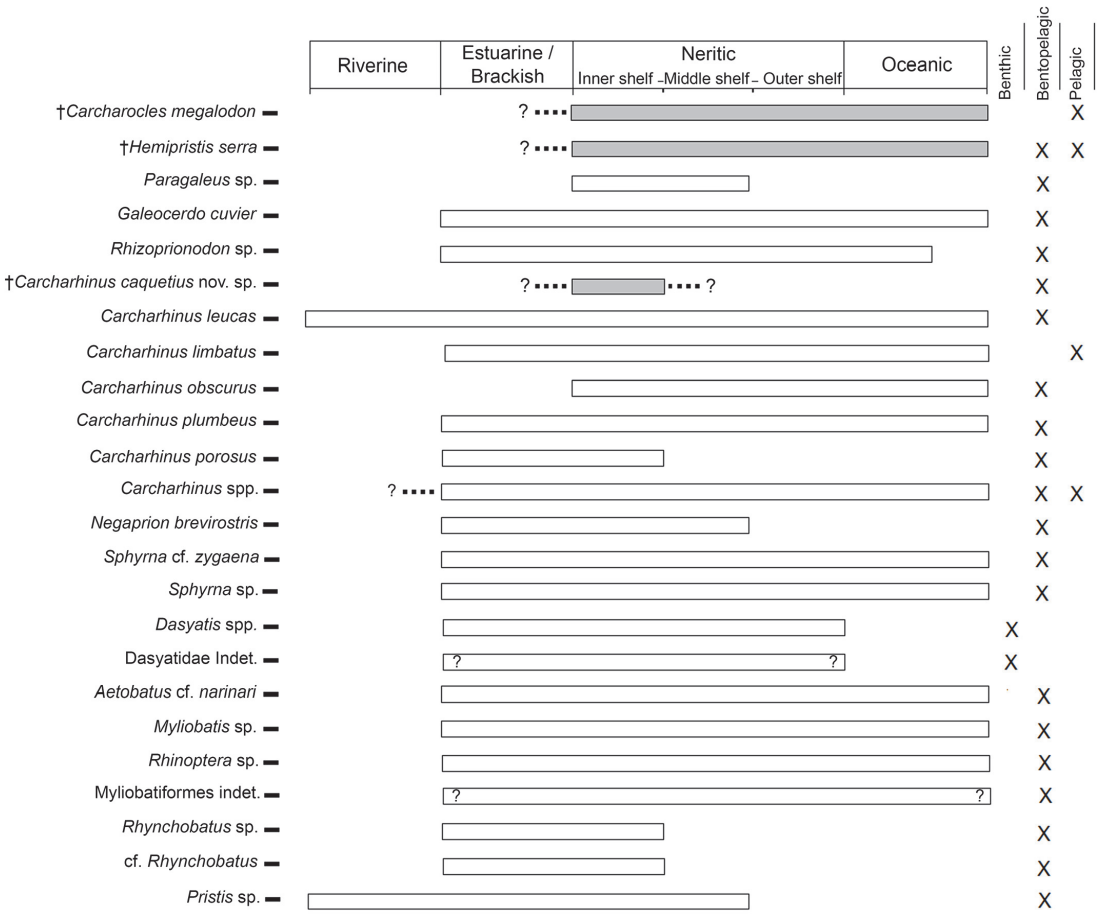

Fig 10. Habitat preferences of Urumaco sequence elasmobranch taxa, based on preferences of extant relatives. Light-gray shading indicates extinct taxa.

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(including the 14 localities included in the present study) (e.g., [19, 26, 29–32, 36, 120]), we hypothesize that the fossil elasmobranch assemblages from the Urumaco sequence are associated primarily with shallow marine and estuarine environments (Fig 11) (S1 Table).

Of the fourteen localities from the Urumaco sequence with associated elasmobranch assemblages (Fig 1 and S1 Table), we suggest that the El Hatillo Norte locality (Urumaco Formation), which is characterized by a coquinoid limestone rich in marine mollusks (currently under study), and Casa el Jebe (Codore Formation) could be indicative of very shallow marine paleoenvironments. The elasmobranch assemblages at other localities of the Urumaco Formation and those of the Socorro Formation (S1 Table) are characterized by the presence of abundant remains of brackish and freshwater fishes, freshwater and marine turtles and crocodilians, and terrestrial and aquatic/semiaquatic mammals [29–32]. The association of this diverse vertebrate fauna suggests paleoenvironments associated with coastal lagoons and estuaries,

Fig 11. Restoration of diverse sharks and rays in coastal lagoon-estuarine at late Miocene times in Urumaco. (**A**) Sharpnose shark *Rhizoprionodon* sp., (**B**) Hammerhead shark *Sphyrna* cf. *zygaena*, (**C**) Bull shark *Carcharhinus leucas*, (**D**) "Big tooth" *Carcharocles megalodon*, (**E**) Tiger shark *Galeocerdo cuvier*, (**F**) Spotted eagle ray *Aetobatus* cf. *narinari*, (**G**) Eagle ray *Myliobatis* sp., (**H**) Guitarfish *Rhynchobatus* sp., (**I**) Sawfish *Pristis* sp., (**J**) Stingray cf. *Dasyatis*. Artwork by Jorge Gonzalez.

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especially the latter environment. Of this fossil aquatic fauna (S2 Table), at least, ten genera of freshwater fishes that includes characins, perciforms, and siluriforms (e.g., [47]), as well the turtle †*Chelus lewisi* Wood, 1976 [121], are phylogenetically close to living groups that occur today in the Orinoco and Amazon drainage systems [20, 30, 47].

The marginal marine paleoenviroments near the mouths of the rivers of the Socorro and Urumaco formations must have been subject to great variability in temperature, pH, sediment load and salinity. This is supported by the abundance in the Urumaco Formation of the foram *Ammonia parkinsoniana* which tolerates a wide range of salinities, and is a dominant taxon in low-salinity lagoons [54]. This suggests that many of the taxa that inhabited these coastal waters may have had broad salinity tolerance (Fig 10). *Galeocerdo cuvier*, *Carcharhinus limbatus*, *C. porosus* and *Negaprion brevirostris* are frequent in estuaries and river mouths, tolerating low levels of salinity, but do not ascend into rivers [43, 44, 46], unlike *Carcharhinus leucas* and *Pristis* species [43, 46, 47]. Batoids such as *Aetobatus narinari*, *Rhinoptera*, *Myliobatis*, and *Dasyatis* are also found in estuaries with low salinity levels [39]; *Rhinoptera bonasus* Mitchill, 1815 [122] even reproduces in the freshwater Maracaibo Lake (Venezuela) [47].

The extinct *Carcharocles megalodon* has been interpreted as a common inhabitant of tropical to warm-temperate coastal-oceanic habitats [2, 23, 24, 123], where it predated primarily cetaceans [81]. Trophic interactions between this large shark (*Carcharocles*) and marine mammals have been inferred based on remains from the early Miocene Cantaure Formation (*Carcharocles chubutensis* Ameghino, 1901[124]) and early Pliocene Paraguaná Formation (*Carcharocles megalodon*), both in Venezuela [15, 17]. However, the presence of *Carcharocles*

in different marine paleoenviroments from the Neogene of Venezuela suggests that this species was a large, transient predator that may have had enough behavioral flexibility to occupy different environments, feeding on fish, turtles, cetaceans and sirenids [15, 17]. In the Urumaco sequence, especially in the Urumaco Formation, we have found isolated teeth of *Carcharocles megalodon* in marine facies and in paleoenviroments interpreted as coastal lagoons and estuaries (S1 Table). In the marine and coastal lagoon facies of the Urumaco Formation, there is no evidence of marine cetaceans; small dolphins probably related to freshwater species that inhabit the Amazon and Orinoco basins are present [30]. The occurrence of *C. megalodon* in the same strata as bony fishes, turtles, sirenids, and crocodiles suggests that these could possibly have been prey for this shark. At present, the presence of *C. megalodon* in freshwater paleoenviroments of the Urumaco sequence cannot be confirmed. Its presence in environments with variable salinity suggests that this taxon had physiological capabilities that allowed it to withstand the variations in salinity in estuarine and possibly river mouth habitats, as do some extant carcharhiniforms [43, 46].

Conclusion

The lithologies of the Urumaco sequence are characterized by substantial variation, indicating the complexity and heterogeneity of these geologic units. Both fossils and the sedimentology document terrestrial and marine facies, including transitional paleoenviroments, and consequently a fauna tolerant to these environments. The elasmobranch fauna from the Urumaco sequence (Socorro-Urumaco-Codore formations), with almost 21 taxa, is associated principally with estuarine coastal lagoon and very shallow marine waters. The presence of elasmobranchs in association with others marine, freshwater and terrestrial vertebrates which provide seemingly contradictory signals for a palaeoenvironmental reconstruction is consistent across the larger stratigraphic sequence. This pattern is not the result of taphonomic processes, but instead proof of mixed coastal marine and fluvial-estuarine hydrographic environments during the Miocene. At the same time, the presence in the Urumaco sequence of abundant aquatic/semiaquatic vertebrates, phylogenetically close to extant groups that occur today in the Orinoco and the Amazon drainage system, support the highly debated hypothesis of a paleohydrographic fluvial, lacustrine or wetland complex drainage flowing along the northwestern coast of the Miocene Falcón basin into the proto-Caribbean.

Supporting Information

S1 Appendix. Geographic coordinates.
(DOC)

S2 Appendix. Referred fossil specimens.
(DOC)

S1 Table. Fossil elasmobranchs from the Urumaco sequence and paleoenvironments
(XLS)

S2 Table. Osteichthyan paleodiversity of the Urumaco sequence (Socorro, Urumaco and Codore formations) and the habitat of their living representatives.
(XLS)

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Author Contributions

Conceived and designed the experiments: JDCB EM MRSV. Performed the experiments: JDCB EM OA MRSV. Analyzed the data: JDCB EM OA MRSV. Contributed reagents/materials/analysis tools: JDCB EM OA RS MRSV. Wrote the paper: JDCB EM OA MRSV.

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S1 Appendix. Geographic coordinates.

Socorro Formation (middle Miocene)

-Cerro Overo (11°11'14"N, 70° 8'44"W)

- Cerro Alto (11°12'30"N, 70° 8'12"W)

Urumaco Formation (late Miocene)

-Sur Quebrada Bejucal (11°11'18"N, 70°15'3"W)

- Quebrada Bejucal (11°11'22"N, 70°15'20"W)

- Puente Río Urumaco (11°12'24"N, 70°15'00"W)

-Domo de Agua Blanca (11°13'25"N, 70°14'5"W)

-El Hatillo (11°14'7"N, 70°15'3"W)

-El Hatillo Norte (11°14'40"N, 70°14'44"W)

-El Mamón (11°14'1"N, 70°16'11"W)

-El Mamón Norte (11°14'27"N, 70°16'2"W)

-El Picache (11°14'26"N, 70°13'27"W)

-Corralito (11°14'57"N, 70°16'9"W)

-Tío Gregorio (11°14'42"N, 70°18'19"W)

Codore Formation (late Miocene–Pliocene)

-Casa El Jebe (11°15'54"N, 70°16'35"W).

S2 Appendix. Referred fossil specimens.

-**Socorro Formation**: *Carcharhinus* spp. [5 teeth (AMU-CURS-630)]; *Negaprion brevirostris* [1 tooth (AMU-CURS-630)]; *Aetobatus* cf. *narinari* [1 teeth (AMU-CURS-323)]; *Myliobatis* sp. [11 teeth (AMU-CURS-322)]; *Rhinoptera* sp. [2 teeth (AMU-CURS-)]; *Pristis* sp. [2 rostra (AMU-CURS-241 and AMU-CURS-639)].

-**Urumaco Formation**: *Carcharocles megalodon* [15 teeth (AMU-CURS-117, 324, 330, 338, 339, 455 and 605; UNEFM-CIAAP-359, 360, 1225, 1226 and 1292; UNEFM-PF-338)]; *Hemipristis serra* [16 teeth (AMU-CURS-331, 332-337 and 362)]; *Paragaleus* sp. [1 tooth (AMU-CURS-640)]; *Galeocerdo cuvier* [2 teeth (AMU-CURS-341 and UNEFM-PF-408)]; *Rhizoprionodon* sp. [11 teeth (AMU-CURS-478, 479-481, 485, 497 and 498)]; *Carcharhinus caquetius* sp. nov. [5 teeth (AMU-CURS-477 and 499)]; *Carcharhinus leucas* [23 teeth (AMU-CURS-355, 360, 363, 364, 368, 458-462)]; *Carcharhinus limbatus* [2 teeth (AMU-CURS-456 and 457)]; *Carcharhinus obscurus* [20 teeth (AMU-CURS-356, 361, 367, 369-371, 463-467)]; *Carcharhinus porosus* [4 teeth (AMU-CURS-472, 473 and 590)]; *Carcharhinus* spp. [77 teeth (AMU-CURS-60, 358, 359, 365, 366, 373-375, 471, 486 and 629)]; *Negaprion brevirostris* [20 teeth (AMU-CURS-342, 343-349, 372, 468-470, 616, 617 and 1039)]; *Sphyrna* cf. *zygaena* [2 teeth (AMU-CURS-474; AMU-CURS-474)]; *Sphyrna* sp. [1 tooth (AMU-CURS-477)]; *Dasyatis* spp. [9 teeth (AMU-CURS-493, 495, 496 and 589)]; Dasyatidae indet. [1 tooth (AMU-CURS-591)]; *Aetobatus* cf. *narinari* [39 teeth (AMU-CURS-272, 273, 275, 276, 308, 311, 313, 318, 329, 488, and 490; UNEFM-CIAAP-1282 and 1288)]; *Myliobatis* sp. [692 teeth (AMU-CURS-59, 61, 260, 262-269, 271, 274, 277, 279, 281-283, 285, 287, 289, 303-307, 312, 314-316, 319, 326, 434, 435, 487, 615 and 618)]; *Rhinoptera* sp. [31 teeth (AMU-CURS-270, 278, 284, 286, 288, 309, 310, 317, 320, 328, 489 and 491)]; Myliobatiformes indet. [5 caudal spines (AMU-CURS-290 and 492)]; *Rhynchobatus* sp. [3 teeth (AMU-CURS-482, 483 and 628)]; *Pristis* sp. [22 rostra (AMU-CURS-23, 40, 41, 43, 45, 102, 107, 235-240, 242, 245, 251 and 376; MCNC-45-72-V, 93-72-V, 99-72-V, 154-72-V and 155-72-V), 41 rostral spines (AMU-CURS-242-244, 246,-251, 327 and 1065), and 4 bucal teeth (AMU-CURS-484)].

-**Codore Formation**: *Carcharocles megalodon* [3 teeth (AMU-CURS-599; UNEFM-PF-351)]; *Hemipristis serra* [3 teeth (AMU-CURS-623)]; *Galeocerdo cuvier* [2 teeth (AMU-CURS-625)]; *Rhizoprionodon* sp. [3 teeth (AMU-CURS-635)]; *Carcharhinus leucas* [5 teeth (AMU-CURS-622)]; *Carcharhinus plumbeus* [4 teeth (AMU-CURS-624)]; *Carcharhinus porosus* [4 teeth (AMU-CURS-632)]; *Negaprion brevirostris* [4 teeth (AMU-CURS-626)]; *Dasyatis* spp. [7 teeth (AMU-CURS-636)]; *Aetobatus* cf. *narinari* [3 fragmented dental plates (AMU-CURS-598), and 14 teeth (AMU-CURS-614)]; *Myliobatis* sp. [95 teeth (AMU-CURS-619)]; *Rhinoptera* sp. [17 teeth (AMU-CURS-621)]; Myliobatiformes indet. [1 caudal spine (AMU-CURS-634)]; cf. *Rhynchobatus* [2 teeth (AMU-CURS-638)]; *Pristis* sp. [1 rostral spine (AMU-CURS-620)].

S1 Table. Fossil elasmobranch from the Urumaco sequence and paleoenvironments.

Taxon	Socorro Formation		Urumaco Formation											Codore Fm
	Middle Mb	Upper Mb	Lower Member		Middle Member		Upper Member							Chiguaje Member
	Cerro Overo	Cerro Alto	Sur Quebrada Bejucal	Quebrada Bejucal	Puente Río Urumaco	Domo de Agua Blanca	El Hatillo	El Hatillo Norte	El Mamón	El Mamón Norte	El Picache	Corralito	Tío Gregorio	Casa El Jebe
†*Carcharocles megalodon*			X	X	X	X	X	X	X		X			X
†*Hemipristis serra*			X	X				X	X		X	X	X	X
Paragaleus sp.									X					
Galeocerdo cuvier								X	X					X
Rhizoprionodon sp.					X		X		X					X
†*Carcharhinus caquetius* nov. sp.					X									
Carcharhinus leucas			X	X				X	X		X	X		X
Carcharhinus limbatus								X			X			
Carcharhinus obscurus					X			X	X		X	X	X	
Carcharhinus plumbeus														X
Carcharhinus porosus					X				X					X
Carcharhinus spp.	X			X	X		X		X			X	X	X
Negaprion brevirostris	X			X				X	X		X	X	X	X
Sphyrna cf. *zygaena*								X	X					
cf. *Dasyatis*					X			X		X				X
Dasyatidae indet.										X				
Aetobatus cf. *narinari*		X			X		X	X	X		X	X	X	X
Myliobatis sp.		X	X	X	X		X	X	X		X	X	X	X
Rhinoptera sp.		X	X	X			X	X				X	X	X
Myliobatiformes indet.									X					X
Rhynchobatus spp.				X				X						X
Pristis sp.	X	X	X		X		X			X	X	X	X	X
Paleoenvironment														
Marine (very shallow waters)								X						X
Coastal lagoon		X			X	X	X		X	X				
Estuarine	X	X	X	X	X		X		X	X	X	X	X	
Riverine														

S2 Table. Osteichthyan paleodiversity of the Urumaco sequence (Socorro, Urumaco and Codore formations) and the habitat of their living representativ

Taxon			Geologic units			Habitat of living representatives		
			Socorro Formation	Urumaco Formation	Codore Formation	Freshwater	Brackish	Marine
Characiformes	Erythrinidae	? *Hoplias*		X		X		
	Serrasalmidae	*Colossoma* sp.		X		X		
		Piaractus sp.		X		X		
Clupeiformes	Engraulidae	Anchoa sp.			X		X	X
		Orthopristis aff. *ruber*			X		X	X
		Cynoscion aff. *jamaicensis*		X			X	X
	Sciaenidae	*Cynoscion* sp.		X	X		X	X
		Equetus sp.		X	X			X
		Larimus sp.		X			X	X
		†*Larimus gatunensis*		X			X	X
		†*Micropogonias coatesi*		X			X	X
		Nebris aff. *Occidentalis*		X			X	X
		†*Ophioscion lundbergi*		X			X	X
		Paralonchurus sp.			X		X	X
		†*Plagioscion urumacoensis*		X		X	X	X
		Epinephelus itajara		X			X	X
	Serranidae	Indt.		X		?	?	?
		Sphyraena sp.			X		X	X
Pleuronectiformes	Cynoglossidae	*Amphiarius rugispinis*		X			X	X
Siluriformes	Ariidae	†*Aspistor verumquadriscutis*		X		X	X	X
		Aspistor quadriscutis		X		X	X	X
		Bagre marinus		X			X	X
		Cathorops sp.		X		X	X	X
		Notarius kessleri		X			X	X
		Notarius troscheli		X			X	X
		Sciades couma		X		X	X	X
		Sciades dowii		X		X	X	?
		Sciades herzbergii		X		X	X	X
		Indt.	X	X		?	?	?
		Doraops cf. *zuloagai*		X		X		
	Doradidae	†*Doras dionae*		X		X		
		Rhinodoras cf. *thomersoni*		X		X		
		Acanthicus sp.		X		X		
	Loricariidae	†*Phractocephalus nassi*		X		X		
	Pimelodidae	*Platysilurus* sp.		X		X		

CHAPTER 5

A new early Miocene (Aquitanian) Elasmobranchii assemblage from the La Guajira Peninsula, Colombia

Kitefin shark *Dalatias* cf. *licha*

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A NEW EARLY MIOCENE (AQUITANIAN) ELASMOBRANCHII ASSEMBLAGE FROM THE LA GUAJIRA PENINSULA, COLOMBIA

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Abstract. Recent field expeditions have led to the discovery of a selachian assemblage from the earliest Miocene (Aquitanian) deposits of the Uitpa Formation in the La Guajira Peninsula, Colombia. This elasmobranch assemblage provides a unique glimpse into the Caribbean biodiversity at the onset of the Neogene. The assemblage consists of 13 taxa, of which some are reported from Miocene deposits for the very first time. There are also new records of taxa the in southern Caribbean region. The taxonomic composition of the selachian assemblage was used to conduct a paleoenvironmental and paleobathymetric analysis of the lower Uitpa Formation. The maximum likelihood estimation of paleobathymetry suggests that the lower part of the Uitpa Formation was probably accumulated at a water depth of 100 to 200 m. This indicates a rapid increase in relative sea level or basin deepening, providing new insights into the possible causes of marine biota changes in the Cocinetas Basin during the Oligocene/Miocene transition.

Key words. Neogene. Tropical America. Caribbean. Sharks. Rays. Paleobathymetry. Paleoenvironments.

Resumen. UN NUEVO ENSAMBLE DE ELASMOBRANCHII DEL MIOCENO TEMPRANO (AQUITANIANO) DE LA PENÍNSULA DE LA GUAJIRA, COLOMBIA. Recientes trabajos de campo han llevado al descubrimiento de un conjunto de seláceos procedente del Mioceno temprano (Aquitaniano) en los depósitos más antiguos de la Formación Uitpa en la Península de La Guajira, Colombia. Este conjunto de elasmobranquios provee una visión única de la paleobiodiversidad del Caribe a inicios del Período Neógeno. El conjunto aquí descrito se compone de 13 taxones, algunos de los cuales son reportados por vez primera para el Mioceno. Esta fauna también incluye nuevos registros para la región sur del Caribe. La composición taxonómica del nuevo ensamble permitió realizar un análisis paleoambiental y paleobatimétrico en la sección más inferior de la Formación Uitpa. La estimación de paleobatimetría usando *maximum likelihood* sugiere que la parte inferior de la Formación Uitpa fue probablemente depositada a profundidades entre los 100 y 200 m. Esto indica un rápido incremento en el nivel relativo del mar o en la profundización de la cuenca, proveyendo nueva información sobre las posibles causas que dieron origen a los cambios en la biota marina de la Cuenca de Cocinetas durante la transición del Oligoceno/Mioceno.

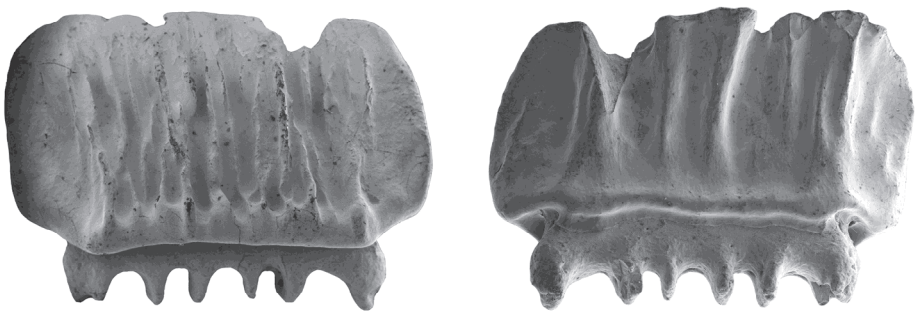
Palabras clave. Neógeno. América Tropical. Caribe. Tiburones. Rayas. Paleobatimetría. Paleoambientes.

THE beginning of the Neogene was a time when world climate was warmer and sea level was higher than at present (Zachos *et al.*, 2001). Large scale geological processes, including the closure of the Central American Seaway and the rise of the Panamanian Isthmus, had not yet been completed (Woodburne, 2010; Montes *et al.*, 2012a,b; Coates and Stallard, 2013; Montes *et al.*, 2015). Large areas of the northern margin of South America were submerged during the early Miocene (see Iturralde-Vinent and MacPhee, 1999 and references therein). This was also the case in the southern Caribbean Cocinetas Basin, where there are widespread early Miocene marine sedimentary deposits that have yielded a rich record of invertebrate (Becker and Dusenbury, 1958; Lockwood, 1965; Rollins, 1965; Thomas, 1972; Hendy *et al.*, 2015) and vertebrate fossils of which most are chondrichthyans (Lockwood, 1965; Moreno *et al.*, 2015).

Early Miocene marine chondrichthyan faunas from Tropical America are still poorly known with only a few relevant reports from Barbados (Casier, 1958), Brazil (Santos and Travassos, 1960; Santos and Salgado, 1971; Reis, 2005; Costa *et al.*, 2009), Cuba (Iturralde-Vinent *et al.*, 1996), Mexico (Gonzales-Barba and Thies, 2000), Panama (Pimiento *et al.*, 2013a), Trinidad (Leriche, 1938), the Grenadines (Portell *et al.*, 2008) and Venezuela (Leriche, 1938; Sánchez-Villagra *et*

CHAPTER 6

An Early Neogene Elasmobranch fauna from the southern Caribbean (Western Venezuela)



Devil ray †*Mobula fragilis*

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An Early Neogene Elasmobranch fauna from the southern Caribbean (Western Venezuela)

Jorge D. Carrillo-Briceño, Orangel A. Aguilera, Carlos De Gracia, Gabriel Aguirre-Fernández, René Kindlimann, and Marcelo R. Sánchez-Villagra

ABSTRACT

The Cantaure Formation (Burdigalian to ?early Langhian) is located in the Falcón Basin, North Western Venezuela, and includes one of the most diverse Neogene teleostean and benthonic invertebrate faunas in Tropical America. The paleoenvironmental preferences of the members of this fauna, as well as published paleogeographic reconstructions, suggest that the Cantaure Formation was deposited in a highly-productive shallow water environment, associated with coastal upwelling. We documented a paleodiversity of 39 shark and ray species, including 15 previously unreported taxa for Venezuela and six for Tropical America. We performed a bathymetric analysis of the fossil assemblage based on the distribution of closely-related extant chondrichthyan relatives of fossil taxa and discuss the ecological role and stratigraphic significance of the latter. Our results support the hypothesis that the Cantaure Formation was deposited in an insular inner-middle shelf environment. The elasmobranch fauna is characterized by a predominance of benthopelagic sharks with piscivorous feeding preferences (e.g., †*Paratodus*, *Galeorhinus*, *Hemipristis*, *Rhizoprionodon*, *Carcharhinus*, *Isogomphodon*, *Negaprion*, †*Physogaleus* and *Sphyrna*) followed by durophagous/cancritrophic feeders (e.g., *Heterodontus*, *Nebrius*, *Mustelus*, *Rhynchobatus*, *Pristis*, *Dasyatis*, cf. *Pteroplatytrygon*, cf. *Taeniurops*, *Aetobatus*, *Aetomylaeus* and *Rhinoptera*). Filter (e.g., *Mobula* and †*Plinthicus*), eurytrophic/sarcophagous (e.g., †*Carcharocles* and *Galeocerdo*) and teuthitrophic (e.g., *Alopias*) feeder species were also found. Teeth of *Carcharocles megalodon* found in Burdigalian sediments of the Cantaure Formation support the presence of this species already in the early Miocene. Some taxa (*Nebrius*, *Carcharhinus* cf. *C. macloti* and *Rhynchobatus*) are absent from the extant Caribbean and Western Atlantic fauna, but were present in the region before the closure of the Central American Seaway.

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INTRODUCTION

Sharks and rays are essential and diverse elements of tropical marine ecosystems (Cortés et al., 2008; Klimley, 2013), and their fossils are ubiquitous in many localities (e.g., Cappetta, 2012). In "Tropical America" – the geographic area of the Western Hemisphere located between the Tropic of Cancer and the Tropic of Capricorn, Neogene chondrichthyan assemblages are known from Barbados (Casier, 1958, 1966), Brazil (Santos and Travassos, 1960; Santos and Salgado, 1971; Reis, 2005; Costa et al., 2009), Cuba (Iturralde-Vinent et al., 1996; MacPhee et al., 2003), Southern Mexico (González-Rodríguez et al., 2013), Panama (Pimiento et al., 2013a), Peru (Alván et al., 2006), Trinidad (Leriche, 1938), The Grenadines (Portell et al., 2008) and Venezuela (Leriche, 1938; Sánchez-Villagra et al., 2000; Aguilera, 2010; Aguilera and Rodrigues de Aguilera, 2004; Aguilera and Lundberg, 2010). Despite all previous efforts, the chondrichthyan fossil record from the Caribbean is still fragmentary and poorly known, making it difficult to reconstruct paleofaunas that could help our understanding of the major ecological and biogeographical changes that happened in the area during the Neogene. Among those changes are those associated with the uplift of the Central American land bridge (Coates and Stallard, 2013; Montes et al., 2015), which interrupted the interoceanic corridor known as the Central American Seaway (CAS), and influenced the water circulation patterns of Pacific and the Caribbean (O´Dea et al., 2007, Leigh et al., 2014). The geographic position of Venezuelan deposits renders them as relevant for investigating the effects of those major paleogeographic rearrangements.

More than 20 years of paleontological expeditions in the Paraguaná Peninsula, North Western Venezuela, produced a collection of 1836 fossil elasmobranch specimens from the Cantaure Formation. This geological unit is thought to have been deposited under fully marine conditions (Díaz de Gamero, 1974; Rey, 1996), exhibiting a well-known high diversity of invertebrates (Ingram, 1947; Jung, 1965; Gibson-Smith, 1974; Gibson-Smith and Gibson-Smith, 1974; Aguilera et al., 2010; Landau et al., in press) and teleostean fishes (Nolf and Aguilera, 1998; Aguilera, 2010; Aguilera and Lundberg, 2010). We hereby present a new taxonomic study of the elasmobranch fauna from the Cantaure Formation and a discussion of the paleoenvironmental and feeding preferences of these elasmobranchs, based on comparisons with extant species.

GEOLOGICAL AND STRATIGRAPHIC SETTING

The Cantaure Formation (Jung, 1965) has been dated as early Miocene, based on biozones of planktonic foraminifera (N7-8) and calcareous nannofossils (NN4-5) (Díaz de Gamero, 1974; Rey, 1996). According to Gradstein et al. (2012), biozones N7 and N8 correspond to the Lower to Middle Miocene transition (upper Burdigalian to lower Langhian). Griffiths et al. (2013) assigned a Burdigalian age (16.5±0.4 Ma.) to a horizon of the Cantaure Formation using Sr isotopes from corals (Figure 1.2). Landau et al. (in press) suggested that the gastropod assemblage from The Cantaure Formation is typical for early-middle Miocene deposits. The stratotype of the Cantaure Formation is located approximately 10 km west of Pueblo Nuevo on the Paraguaná Peninsula, Falcón State, Venezuela. Outcrops are found south of Casa Cantaure (Figure 1.1) and are composed of fossiliferous silty shales interbedded with thin algal limestones and shell beds (Hunter and Bartok, 1974). Jung (1965) estimated a thickness of 75 m for the composit section of the Cantaure Formation. Hunter and Bartok (1974) divided the Cantaure Formation into three sections: 1) fossiliferous basal breccia unconformably overlaying the granite basement, 2) lower section comprised mainly of

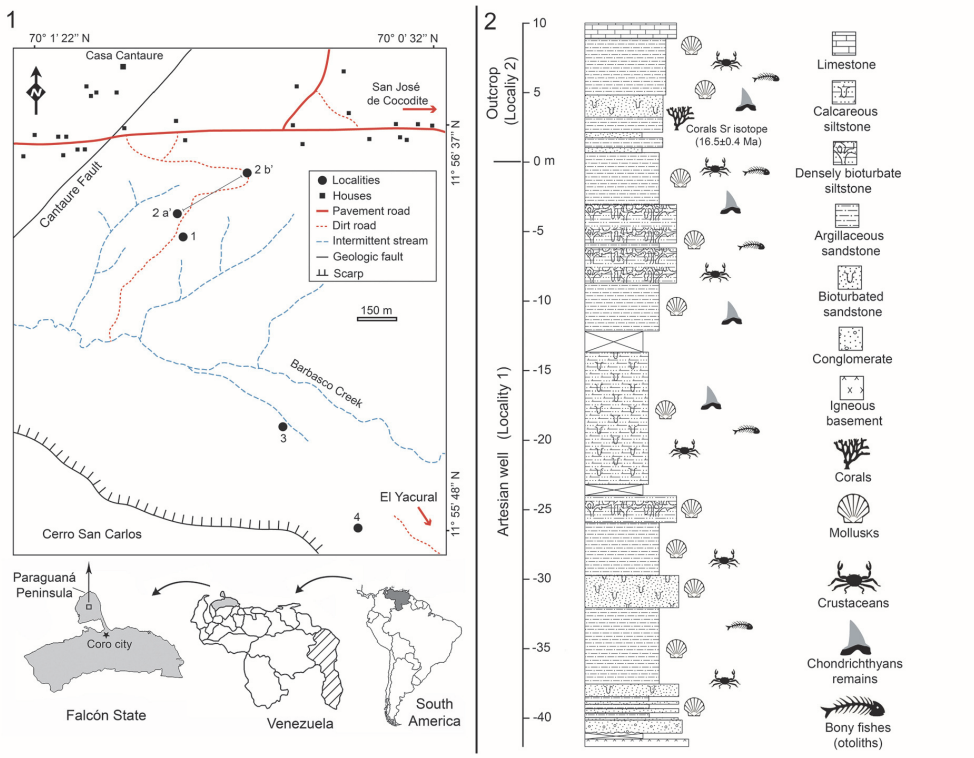

FIGURE 1. Location and stratigraphy of the Cantaure Formation. 1. Fossiliferous localities. 2. Stratigraphic section of locality 1 (artesian well) and locality 2 (outcrop). Stratigraphic column modified after Aguilera (2010) and Aguilera et al. (2013).

shales and some sandy horizons [including the mollusk rich horizons illustrated by Jung (1965)], and 3) upper section represented by silty shales interbedded with thin algal limestones and shell beds. However, Hunter and Bartok (1974) did not provide a stratigraphic column, while they mentioned that the landscape of the area prevents a detailed measurement of the complete section. In contrast, Rey (1996) constructed a stratigraphic column of the suggested basal and middle sections, and also assumed that the mollusks described by Jung (1965), Gibson-Smith (1974) and Gibson-Smith and Gibson-Smith (1974), were derived from the upper section.

The top of the Cantaure Formation is conformably overlain by limestone layers that have been interpreted by Jung (1965) and Hunter and Bartok (1974) as post-Cantaure and pre-Pliocene sedimentation. Rey (1996) suggested that the upper contact of the Cantaure Formation represents an unconformity with the Amuay Member (early Pliocene) of the Paraguaná Formation. Our field observations (OAA, JDCB, pers. obs.) indicate possible lateral variations in a short distance, with fossiliferous outcrops (e.g., thick layers of barnacles) that are not exposed in the previously known and described fossiliferous localities (e.g., Jung, 1965; Hunter and Bartok, 1974; Rey, 1996, among others). All the above clearly indicates that the Cantaure Formation is a more complex sequence than previously thought, in need of a new, detailed stratigraphic redescription.

MATERIAL AND METHODS

The fossil elasmobranch fauna described here (Table 1; Appendix 1) consists of 1836 specimens from four localities in the Cantaure Formation (Figure 1.1), which have been collected by the authors and other collaborators during several expeditions since 1992. Locality 1 (11° 56' 20" N, 70° 1' 2" W) corresponds to an artesian well ~44 m deep (Figure 1.2) and locality 2 (a': 11° 56' 23" N,

TABLE 1. Elasmobranchii paleodiversity of the Cantaure Formation.

Superorder	Order	Family	Genus	Taxon
Galeomorphii	Heterodontiformes	Heterodontidae	*Heterodontus*	*Heterodontus* sp.
	Orectolobiformes	Ginglymostomatidae	*Nebrius*	*Nebrius* sp.
	Lamniformes	†Otodontidae	†*Paratodus*	†*Paratodus benedenii* (Le Hon, 1871)
			†*Carcharocles*	†*Carcharocles megalodon* (Agassiz, 1843)
		Alopiidae	*Alopias*	*Alopias* cf. *A. vulpinus* (Bonnaterre, 1788)
	Carcharhiniformes	Triakidae	*Galeorhinus*	*Galeorhinus* cf. *G. galeus* (Linnaeus, 1758)
			Mustelus	*Mustelus* sp.
		Hemigaleidae	*Hemipristis*	†*Hemipristis serra* (Agassiz, 1835)
		Carcharhinidae	*Galeocerdo*	†*Galeocerdo aduncus* Agassiz, 1843
				†*Galeocerdo mayumbensis* Dartevelle and Casier, 1943
			Rhizoprionodon	*Rhizoprionodon* sp.
			Carcharhinus	†*Carcharhinus ackermannii* Santos & Travassos, 1960
				Carcharhinus brachyurus(Günther, 1870)
				Carcharhinus falciformis(Müller and Henle, 1839)
				Carcharhinus cf. *C. galapagensis* (Snodgrass and Heller, 1905)
				†*Carcharhinus gibbesii* (Woodward, 1889)
				Carcharhinus cf. *C. limbatus* (Müller and Henle, 1839)
				Carcharhinus cf. *C. macloti* (Müller and Henle, 1839)

70° 1' 3" W and b': 11° 56' 2" N, 70° 0' 55" W) is an outcrop (overlying the section of locality 1) with a ~300 m long collecting surface (Figures 1.1-1.2). The corals used by Griffiths et al. (2013) for Sr isotope analysis were collected at locality 2 (Figure 1.1-1.2). This suggests that localities 1 and at least the lower section of locality 2 are of Burdigalian age (Figure 1.2). Localities 3 (11° 55' 59" N, 70° 1' 1" W) and 4 (11° 55' 48" N, 70° 00' 40" W) correspond to surface collecting areas along the south of Barbasco Creek, on the north escarpment of the Cerro San Carlos (Figure 1.1). Without a detailed stratigraphical knowledge of the outcrops south of Barbasco Creek, it is not possible to establish if localities 3 and 4 are different vertical strata (facies) along the Cantaure section or horizontal variations of localities 1 and 2. Field observations (OAA, JDCB and GAF pers. obs.) suggest that localities 3 and 4 are stratigraphically older than the limestones layers attributed to post-Cantaure sedimentation (Jung, 1965; Hunter and Bartok, 1974).

Large specimens were surface-collected directly from the outcrop, while microsamples were collected after screen-washing approximately 1000 and 380 kg of sediments (mesh sizes: 0.5 and 2 mm) from locality 1 and 2, respectively. Approximately 50 kg of sediment was processed from locality 3, but it did not contain otoliths or elasmobranch micro-teeth. Specimens from locality 4 were only surface collected. The Cantaure specimens (Appendix 2) are housed in the paleontological collections of the Alcaldía Bolivariana de Urumaco (AMU-CURS), Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas of the Universidad Experimental Francisco de Miranda (CIAAP, UNEFM-PF), and the Museo de Ciencias de Caracas (MCNC), all in Venezuela.

TABLE 1 (continued).

Superorder	Order	Family	Genus	Taxon
				Carcharhinus perezi (Poey, 1876)
				Carcharhinus sp. 1
				Carcharhinus spp.
			Isogomphodon	†*Isogomphodon acuarius* (Probst, 1879)
			Negaprion	†*Negaprion eurybathrodon* (Blake, 1862)
			†*Physogaleus*	†*Physogaleus contortus* (Gibbes, 1849)
			Gen. indet.	sp. indet.
		Sphyrnidae	*Sphyrna*	†*Sphyrna arambourgi* Cappetta, 1970
				Sphyrna cf. †*S. laevissima* (Cope, 1867)
Batomorphii	Rajiformes	Rhynchobatidae	*Rhynchobatus*	*Rynchobatus* sp.
		Pristidae	*Pristis*	*Pristis* sp.
	Myliobatiformes	Dasyatidae	*Dasyatis*	*Dasyatis* sp.
			cf. *Pteroplatytrygon*	cf. *Pteroplatytrygon* sp.
			cf. *Taeniurops*	cf. *Taeniurops* sp.
				Dasyatidae Indet.
		Myliobatidae	*Aetobatus*	*Aetobatus* sp.
			Aetomylaeus	*Aetomylaeus* sp.
		Rhinopteridae	*Rhinoptera*	*Rhinoptera* sp.
		Mobulidae	*Mobula*	†*Mobula fragilis* (Cappetta, 1970)
				Mobula cf. †*M. loupianensis* (Cappetta, 1970)
				Mobula sp.
			†*Plinthicus*	†*Plinthicus stenodon* Cope, 1869
				Myliobatiformes indet.
				Chondrichthyes indet.

The taxonomy follows Cappetta (2012) and Compagno (2005), with the exception of the extinct genus *Carcharocles* Jordan and Hannibal, 1923, for which we follow the nomenclature of Pimiento et al. (2010). Taxonomic identification was based on an extensive literature review, and also comparative analyses between fossil and recent specimens from the following collections: Mapuka Museum of Universidad del Norte (MUN-STRI), Barranquilla, Colombia; Museu Paraense Emilio Goeldi (MPEG-V), Belem, Brazil; Natural History Museum of Basel (NMB), Switzerland; Paleontological collection of the Institut des Sciences de l' Evolution, University of Montpellier (UM), France; Palaeontological Institute and Museum at the University of Zurich (PIMUZ), Switzerland and René Kindlimann private collection, Uster, Switzerland.

We analyzed the abundance using percentages of specimens by order, families and species using the 39 securely recognized taxa that are represented by 1711 specimens (out of the 1836 collected in total) (Appendix 1). For conducting the paleoecological interpretation, we compiled information on habitat preference (benthic, benthopelagic, pelagic, neritic and bathyal) and feeding ecology (dietary composition and behavior) of extant taxa recorded in the Cantaure Formation (Appendix 3), following Compagno (1984a, 1984b); Cortés (1999); Compagno et al. (2005); Musick et al. (2004); Kiraly et al. (2003); Voigt and Weber (2011); Cortés et al. (2008); Ebert and Stehmann (2013); and the FishBase website (Froese and Pauly, 2015). The paleobathymetric analysis was performed following the methodology of Nolf and Brzobohatý (1994), adapted to fossil sharks (Carrillo-Briceño et al., 2015a, 2016). For this analysis we included only species/genera with closely related extant taxa. Extinct species and taxa with-

out clear identification to genus were removed from the analysis. A total of 34 (out of 39) taxa, for which ecological information is available, were analyzed.

Taking into consideration the limitations associated with paleoecological interpretations of fossil assemblages, we tried to approach the ecological role that members of the Cantaure elasmobranch fauna played in this ancient marine environment. We use the categorization of elasmobranch feeding preferences suggested by Cortés (1999) and Cortés et al. (2008). Living sharks and rays as a whole exhibit a wide range of diets, but each species has specific preferences. The latter are used to infer the diet of taxa we documented from the Cantaure assemblage (Appendix 3).

RESULTS

Taxonomical Composition

The taxonomical composition of the four study localities includes at least 39 species of galeomorphs and batoids (Table 1; Appendix 1, 4). Galeomorphs are represented by 26 species, 15 genera and eight families of Heterodontiformes, Orectolobiformes, Lamniformes and Carcharhiniformes (Table 1; Figure 2). Batoids include 13 species attributed to 10 genera and six families of Rajiformes and Myliobatiformes (Table 1; Figure 2). Pictures of the chondrichthyan teeth, vertebrae and caudal and rostral denticles in Figures 3-12, were illustrated following the taxonomic classification shown in Table 1.

Heterodontiformes Berg, 1937. The record of this group (Heterodontidae Gray, 1851) consists of a single and undetermined specimen of *Heterodontus* Blainville, 1816. The tooth was collected from locality 2 (Appendix 1, 4), and was previously reported by Aguilera and Lundberg (2010) and Aguilera (2010). The specimen is missing from the UNEFM collection and it is not illustrated here.

Orectolobiformes Applegate, 1972. The orectolobiform specimens are characterized by a long apron and a short main cusp flanked by more than seven pairs of lateral cusplets (Figure 3.1-3.9). This condition is diagnostic for *Nebrius* Rüppell, 1837, a genus recorded from North America going back to the Eocene (e.g., Kent, 1994; Müller, 1999). The specimens from the Cantaure assemblage (Figure 3.1-3.9; Appendix 1, 4) were previously assigned to *Ginglymostoma delfortriei* (Daimeries, 1889) (Aguilera and Rodrigues de Aguilera, 2004; Aguilera, 2010; Aguilera and Lundberg, 2010). Fossils of *Nebrius* in the Americas have not been thoroughly studied, and there is no clear consensus about their taxonomy at the species level or stratigraphic range (e.g., Kent, 1994; Cicimurri and Knight, 2009). Therefore we refrain from assigning species to our specimens. Cicimurri and Knight (2009) suggested that some fossil teeth of *Nebrius* (from North America) have been misidentified as *Ginglymostoma* Müller and Henle, 1837. The specimens referred to *G. delfortriei* from Panama (Pimiento et al., 2013b) and *Ginglymostoma* sp. from Brazil (Costa et al., 2009) resemble our *Nebrius* teeth from the Cantaure Formation.

Lamniformes Berg, 1937. These sharks are represented by one species of Alopiidae Bonaparte, 1838 and two genera and two species of †Otodontidae Glikman 1964 (Figure 2). *Alopias* cf. *A. vulpinus* (Bonnaterre, 1788) is represented by three specimens (Figure 3.22-3.26; Appendix 1, 3) while the otodontid †*Paratodus benedenii* (Le Hon, 1871) is the least abundant lamniform (Figure 3.10-3.11; Appendix 1, 4). The most abundant lamniform is the otodontid †*Carcharocles megalodon* (Agassiz, 1843), with more than 100 specimens (Figure 3.12-3.21) from all studied localities (Appendix 1, 4). Many *C. megalodon* teeth are broken; however, most of them, especially large specimens, preserve the wide triangular shape (crown without lateral cusplets), a v-shaped 'neck', a fine serrations, and the large size that characterize this species (Purdy et al., 2001; Cappetta, 2012; Pimiento et al., 2010, 2013b). Small teeth having a pair of short lateral cusplets may belong to juvenile and/or subadult individuals of *C. megalodon* (Figure 3.12-3.16), a feature not present in adult teeth (Figure 3.17-3.21). Morphologically, the younger species *Carcharocles chubutensis* (Ameghino, 1901), differs from *C. megalodon* by the presence of lateral cusplets not separated from the crown on the teeth of juveniles, subadults and adults (Cappetta, 2012; Pimiento et al., 2013a). In more derived populations as *C. megalodon*, lateral cusplets disappear, except sometimes on very lateral files or in juvenile individuals (Cappetta, 2012). This absence of lateral cusplets in *C. megalodon* adult teeth has been interpreted as the result of heterochronic processes in the *Carcharocles* clade through geologic time (Pimiento et al., 2010, 2013a, 2013b; Pimiento and Balk, 2015). The absence of lateral cusplets in all well-preserved teeth interpreted as adults (including also some teeth that may belong to juvenile/subadults specimens) allows us to assign our specimens to *C. megalodon*. In addition, adult teeth of *C. megalodon* referred here, are very similar to those of the

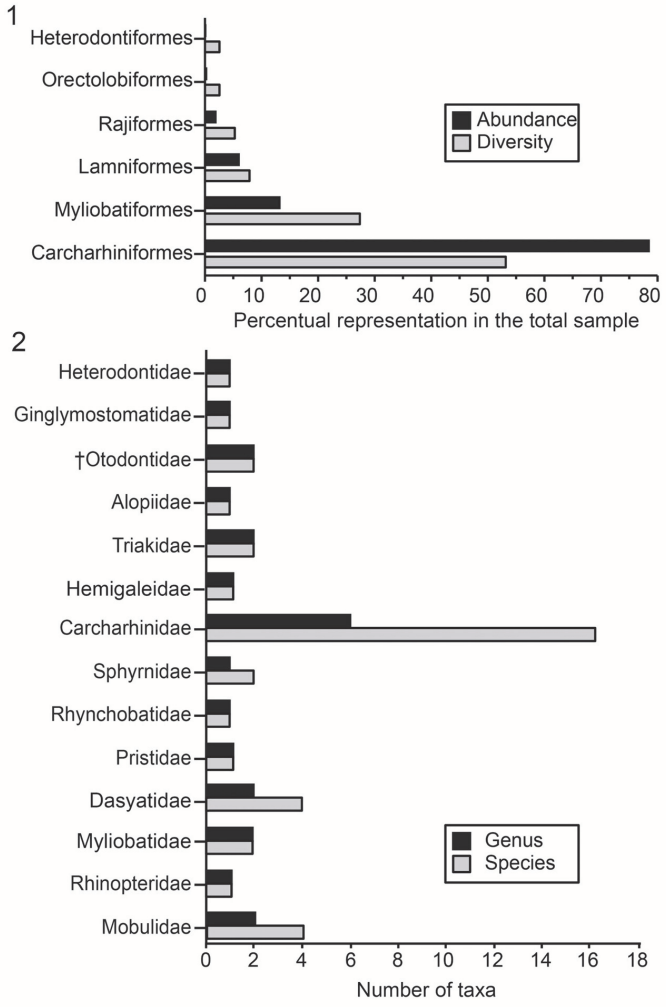

FIGURE 2. Elasmobranch paleodiversity of the Cantaure Formation. 1. Orders and 2. Families and genera.

same species, found in the late Burdigalian section (~16.2 Ma.) of the Castilletes Formation at North East Colombia (under study by JDCB).

Carcharhiniformes Compagno, 1973. This order is represented by four families, 10 genera and 21 species, thus being the most abundant and diverse one of the Cantaure assemblage (Figures 2, 4-8; Table 1; Appendix 1, 4). Triakidae Gray, 1851 [two genera and two species: *Galeorhinus* cf. *G. galeus* (Linnaeus, 1758) (Figure 4.1-4.2), and *Mustelus* Linck, 1790 (*Mustelus* sp.) (Figure 4.3-4.7)], Hemigaleidae Hasse, 1879 [†*Hemipristis serra* (Agassiz, 1835) (Figure 4.8-4.13)], and Sphyrnidae Gill, 1872 [†*Sphyrna arambourgi* Cappetta, 1970 (Figure 7.21-7.25), and *Sphyrna* cf. †*S. laevissima* (Cope, 1867) (Figure 8.1-8.5)], are the less diverse families of this order in the Cantaure assemblage (Figure 2; Appendix 1, 4). Nevertheless, *Hemipristis serra* with 425 specimens (Appendix 1, 4), is the second most abundant species of the assemblage, representing 23% of the total specimens collected. The specimen referred by Aguilera and Rodrigues de Aguilera (2004) to *Paragaleus* sp. corresponds to a juvenile posterior ?lower tooth of *H. serra* (Figure 4.8).

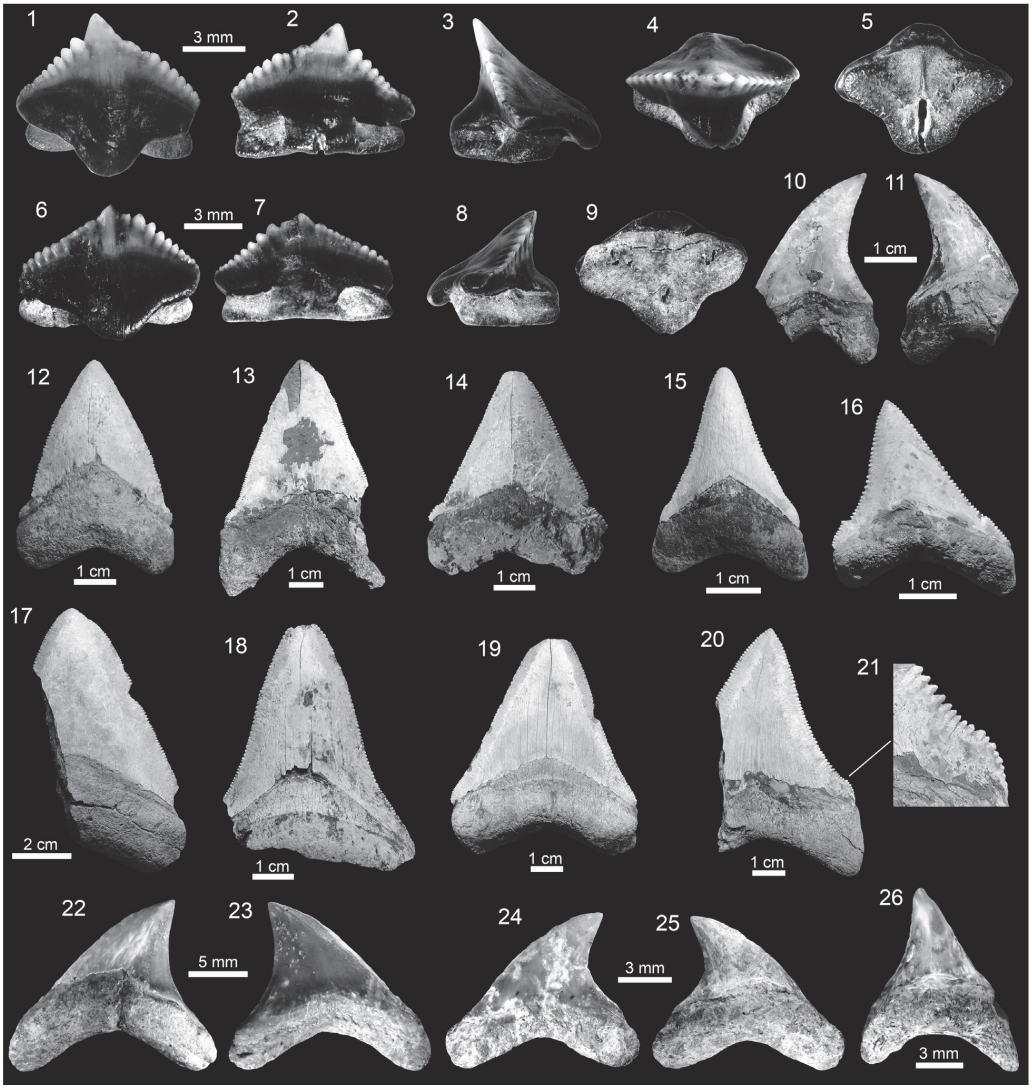

FIGURE 3. Orectolobiformes and Lamniformes of the Cantaure Formation. 1-9. *Nebrius* sp. (AMU-CURS-986); 10-11. †*Paratodus benedenii* (AMU-CURS-645). 12-21. †*Carcharocles megalodon* (12: AMU-CURS-997; 13: AMU-CURS-512; 14: UNEFM-PF-349; 15: AMU-CURS-996; 16: AMU-CURS-518; 17-18: UNEFM-PF-s/n; 19: AMU-CURS-512 and 20-21: AMU-CURS-515). 22-26. *Alopias* cf. *A. vulpinus* (22-23: AMU-CURS-985; 24-25: AMU-CURS-983 and 26: AMU-CURS-984). Jaw position: upper (10-11? 12, 14? 17, 22-25), lower (13, 15, 18) and indet. (1-9, 16, 19-21, 26). View: labial (1, 6, 10, 13, 20-21, 23, 24), lingual (2, 7, 11-12, 14-19, 22, 25-26), profile (3, 8), occlusal (4) and basal (5, 9).

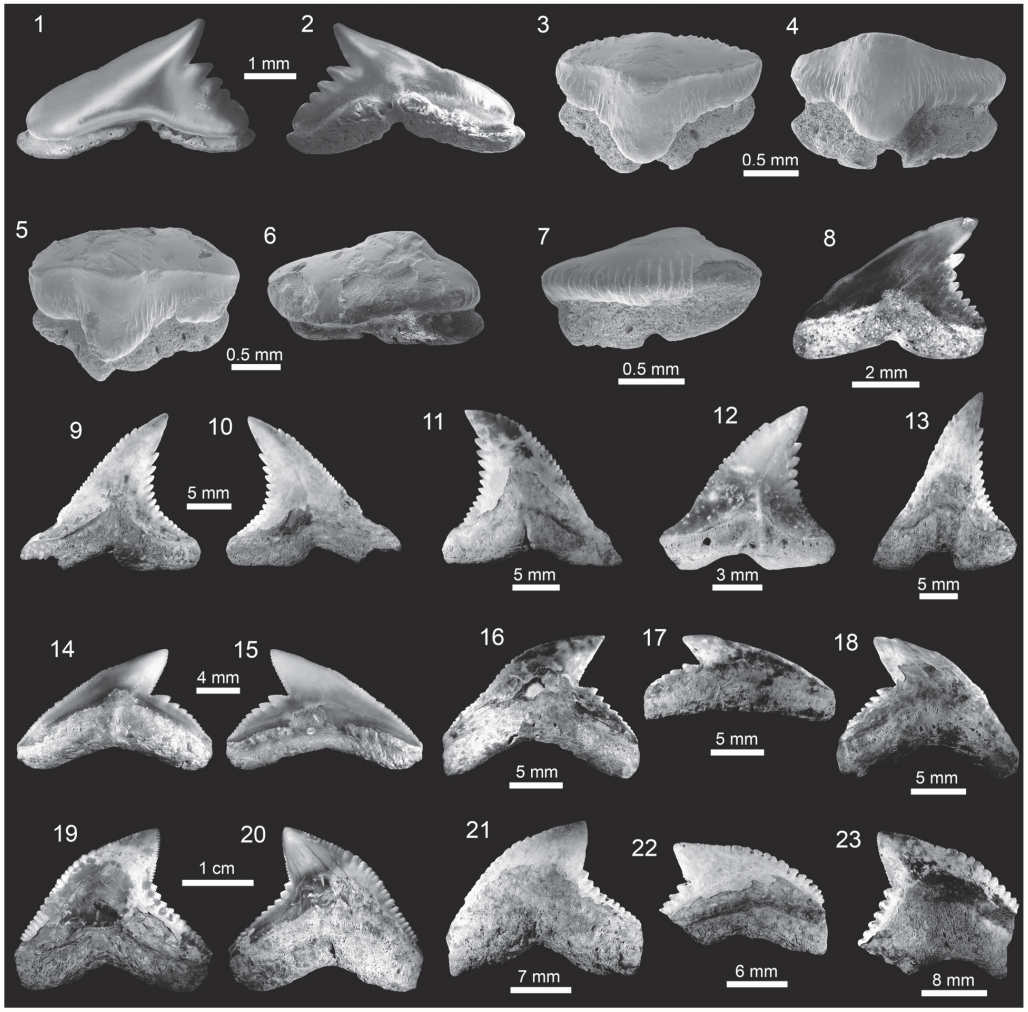

FIGURE 4. Carcharhiniformes of the Cantaure Formation. 1-2. *Galeorhinus* cf. *G. galeus* (AMU-CURS-974). 3-7. *Mustelus* sp. (AMU-CURS-975). 8-13. †*Hemipristis serra* (8: AMU-CURS-731 and 9-13: AMU-CURS-644). 14-18. †*Galeocerdo aduncus* (14-15: AMU-CURS-730 and 16-18: AMU-CURS-647). 19-23. †*Galeocerdo mayumbensis* (19-20: AMU-CURS-995 and 21-23: AMU-CURS-646). Jaw position: upper (9-12), lower (8? 13) and indet. (1-7, 14-23). View: labial (1, 6, 7, 10, 15, 19, 21-22), lingual (2, 4, 8-9, 11-14, 16-18, 20, 23) and occlusal-lingual (3, 5).

The Carcharhinidae Jordan and Evermann, 1896, with six genera and 16 species, is the most diverse and abundant family of the assemblage (Figure 2; Table 1; Appendix 1, 4). The genera *Rhizoprionodon* Whitley, 1929 [*Rhizoprionodon* sp. (Figure 5.1-5.5)], *Isogomphodon* Gill, 1862 [†*Isogomphodon acuarius* (Probst, 1879) (Figure 7.1-7.5)], *Negaprion* Whitley, 1940 [†*Negaprion eurybathrodon* (Blake, 1862) (Figure 7.6-7.10)], and †*Physogaleus* Cappetta, 1980 [†*Physogaleus contortus* (Gibbes, 1849) (Figure 7.11-7.15)], are represented by one species each. *Galeocerdo* Müller and Henle, 1837 is represented by two species [†*Galeocerdo aduncus* Agassiz, 1843 (Figure 4.14-4.18), and †*Galeocerdo mayumbensis* Dartevelle and Casier, 1943 (Figure 4.19-4.23)]. *Negaprion eurybathrodon* with 586 specimens (Appendix 1, 4) is the most abundant species of the assemblage,

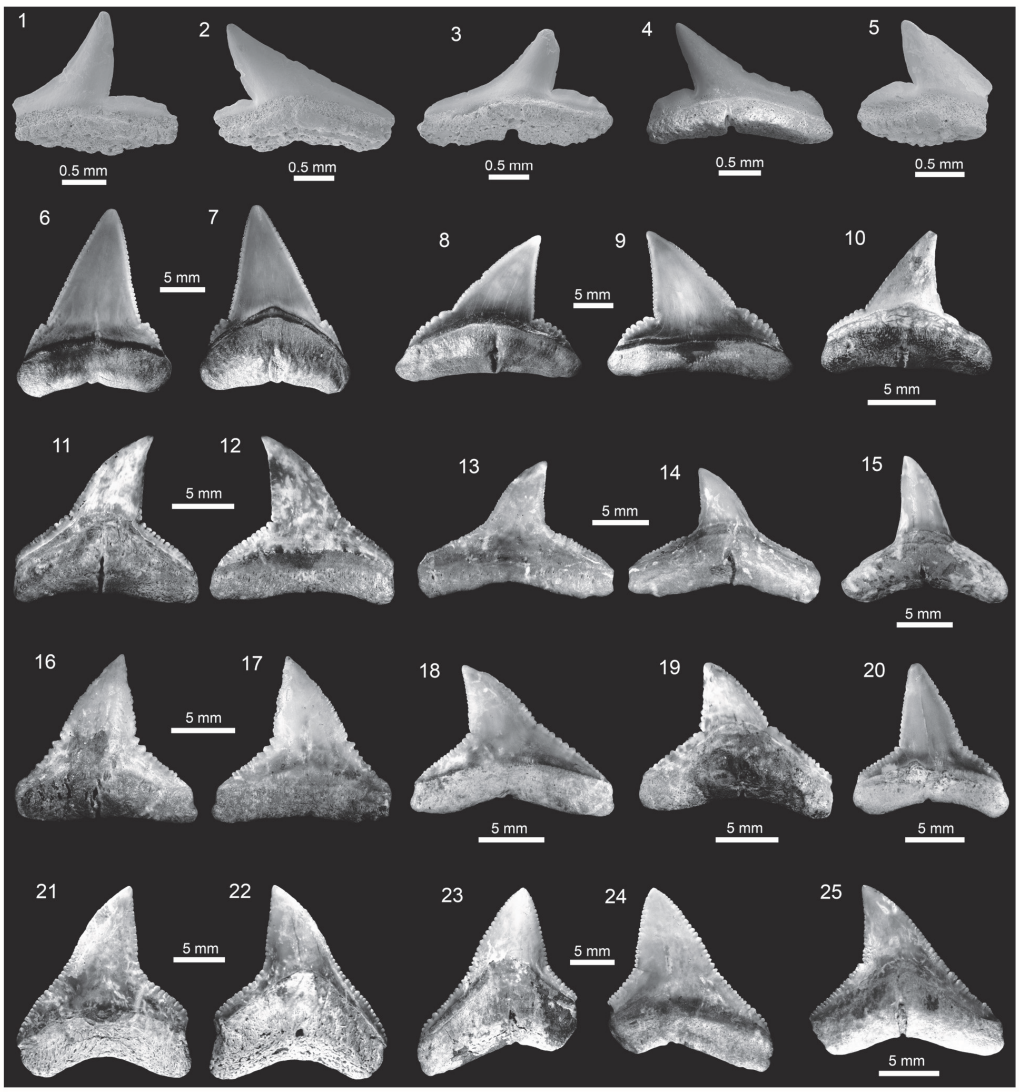

FIGURE 5. Carcharhiniformes of the Cantaure Formation. 1-5. *Rhizoprionodon* sp. (1-3, 5: AMU-CURS-975 and 4: AMU-CURS-960). 6-10. †*Carcharhinus ackermannii* (6-7: AMU-CURS-713 and 8-10: AMU-CURS-714). 11-15. *Carcharhinus brachyurus* (AMU-CURS-990). 16-20. *Carcharhinus falciformis* (AMU-CURS-991). 21-25. *Carcharhinus* cf. *C. galapagensis* (AMU-CURS-973). Jaw position: upper (2, 4-14, 16-25) and lower (1, 3. 15). View: labial (6, 9, 12-13, 17-18, 20-21, 24) and lingual (1-5, 7-8, 10-11, 14-16, 19, 22-23, 25).

representing 32% of the total specimens collected. Specimens referred to *Mustelus* sp. (Triakidae) and *Rhizoprionodon* sp. (Carcharhinidae), are few and fragmentary, lacking diagnostic characters for accurate species assignment.

The genus *Carcharhinus* Blainville, 1816, with nine species, represents the most diverse genus from the Cantaure assemblage (Figures 2, 5.6-5.25, 6.1-6.24; Table 1; Appendix 1, 4). With the exception of the extinct †*Carcharhinus ackermannii* Santos and Travassos, 1960 (Figure 5.6-5.10) and †*Carcharhinus gibbesii* (Woodward, 1889) (Figure 6.1-6.4), the species *Carcharhinus brachyurus* (Günther, 1870) (Figure 5.11-5.15),

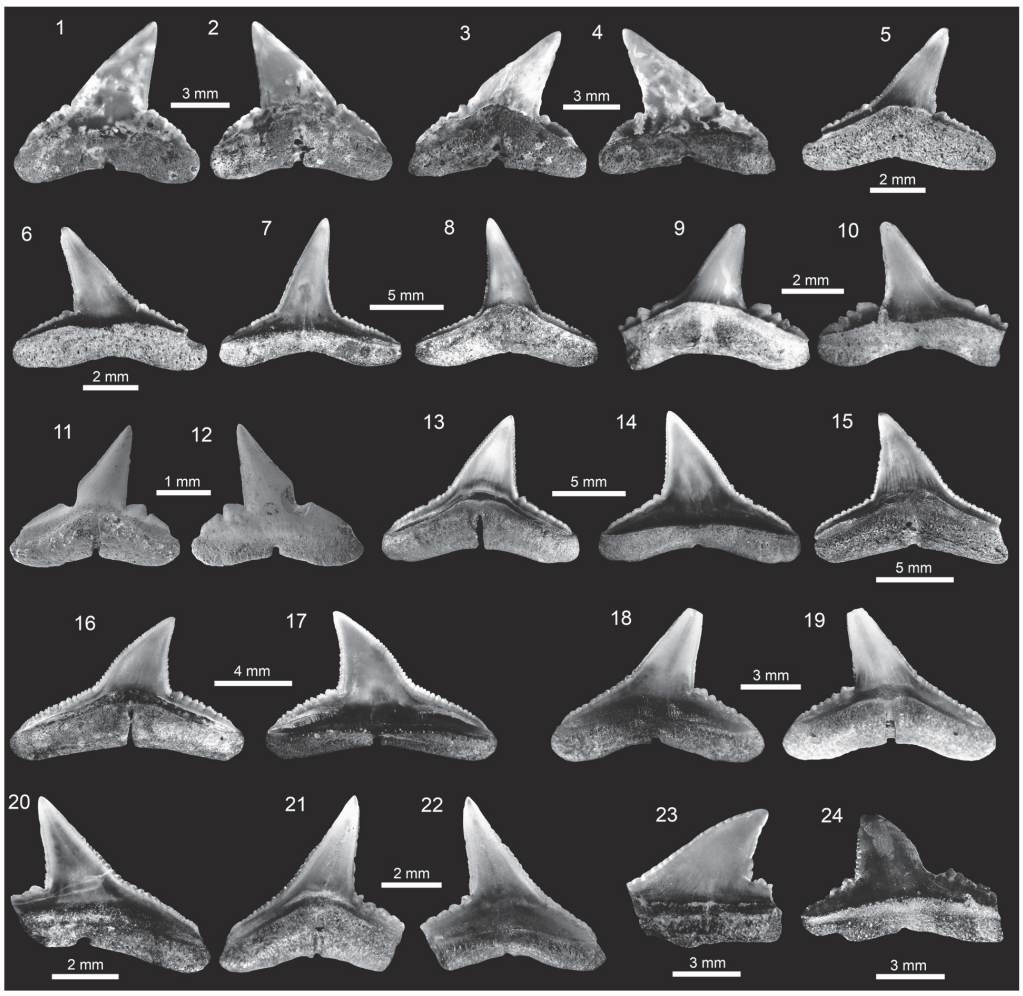

FIGURE 6. Carcharhiniformes of the Cantaure Formation. 1-4. †*Carcharhinus gibbesii* (AMU-CURS-958). 5-8. *Carcharhinus* cf. *C. limbatus* (AMU-CURS-944). 9-12. *Carcharhinus* cf. *C. macloti* (AMU-CURS-957). 13-17. *Carcharhinus perezi* (AMU-CURS-956). 18-22. *Carcharhinus* sp.1 (AMU-CURS-943). 23-24. *Carcharhinus* spp. (23: AMU-CURS-941 and 24: AMU-CURS-940). Jaw position: upper (1-24). View: labial (1, 4, 6-7, 10, 12, 14, 17-18, 20, 22-24) and lingual (2-3, 5, 8-9, 11, 13, 15-16, 19, 21).

Carcharhinus falciformis (Müller and Henle, 1839) (Figure 5.16-5.20), *Carcharhinus* cf. *C. galapagensis* (Snodgrass and Heller, 1905) (Figure 5.21-5.25), *Carcharhinus* cf. *C. limbatus* (Müller and Henle, 1839) (Figure 6.5-6.8) and *Carcharhinus perezi* (Poey, 1876) (Figure 6.13-6.17), have living counterparts and most of them inhabit the Atlantic and Pacific coast of America (Compagno et al., 2005). *Carcharhinus macloti* (Müller and Henle, 1839) (Figure 6.9-6.12) is today an exclusive inhabitant of the Indo-west Pacific Ocean (Compagno et al., 2005). The specimens referred to *Carcharhinus* sp.1 (Figure 6.18-6.22), have a dental morphology different, especially in the form of the crown, which differentiate these teeth from the rest of the *Carcharhinus* species found in the Cantaure assemblage. Due to the scarcity of specimens (Appendix 1) and the lack of preserved diagnostic characters in *Carcharhinus* teeth we have used for comparison (fossil and recent speci-

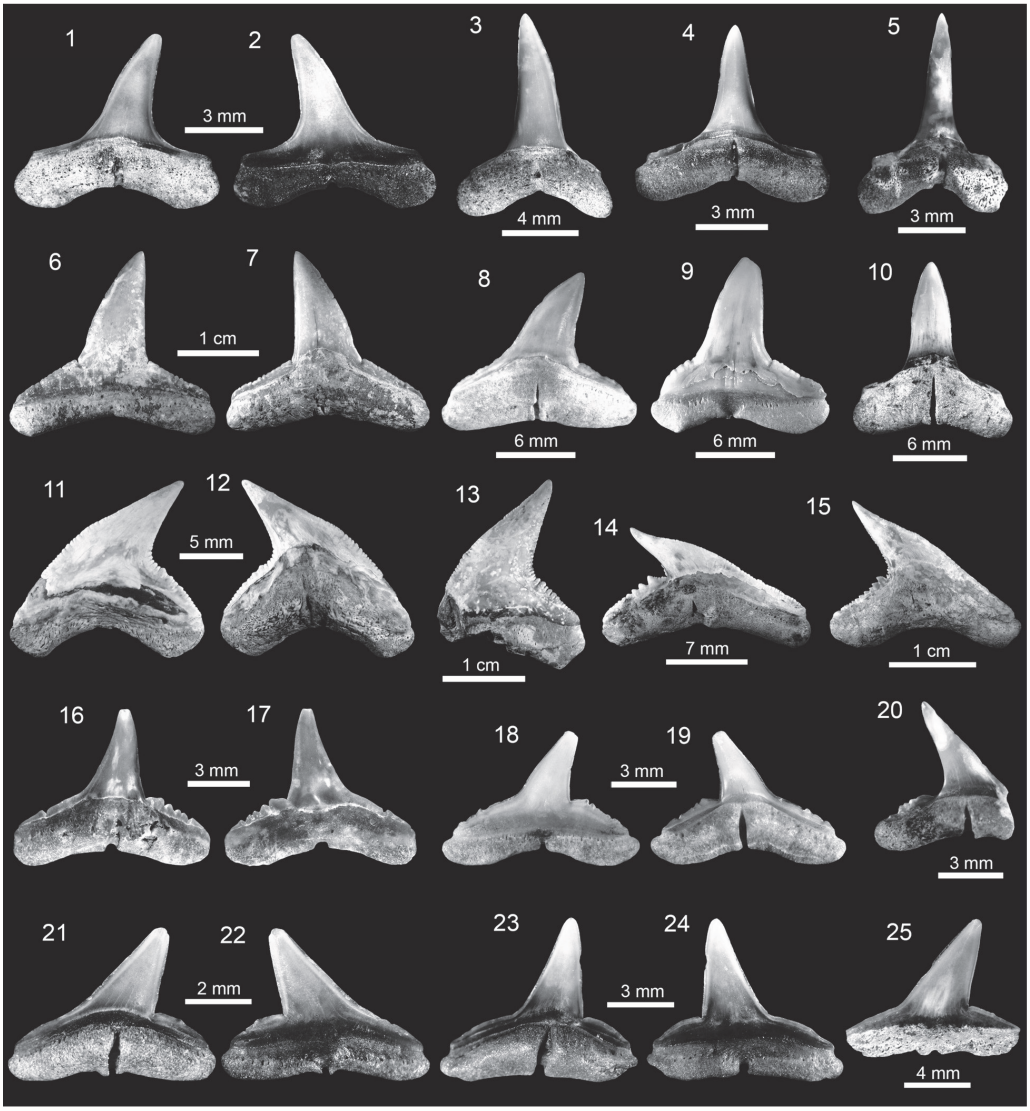

FIGURE 7. Carcharhiniformes of the Cantaure Formation. 1-5. †*Isogomphodon acuarius* (1-2: AMU-CURS-950 and 3-5: AMU-CURS-951). 6-10. †*Negaprion eurybathrodon* (6-9: AMU-CURS-989 and 10: AMU-CURS-987). 11-15. †*Physogaleus contortus* (11-12: AMU-CURS-719 and 13-15: AMU-CURS-648). 16-20. Carcharhinidae indet. (AMU-CURS-939). 21-25. †*Sphyrna arambourgi* (21-24: AMU-CURS-961 and 25: AMU-CURS-962). Jaw position: upper (1-3, 6-9, 16-19? 21-22, 25), lower (4-5, 10, 20? 23-24) and indet. (11-15). View: labial (2, 6, 9, 11, 13, 17-18, 22, 24-25) and lingual (1, 3-5, 7-8, 10, 12, 14-16, 19-21, 23).

mens), we prefer to keep these specimens to a generic level. We have referred all specimens that are broken and eroded, without any diagnostic features for specific identification (Figure 6.23-6.24), to *Carcharhinus* spp. Some of the specimens classified as Carcharhinidae indet. (Figure 7.16-7.20; Table 1; Appendix 1, 4), exhibit a very prominent lingual protuberance with a sigmoid cusp, which could be the basis of a more detailed taxonomical identification in future studies.

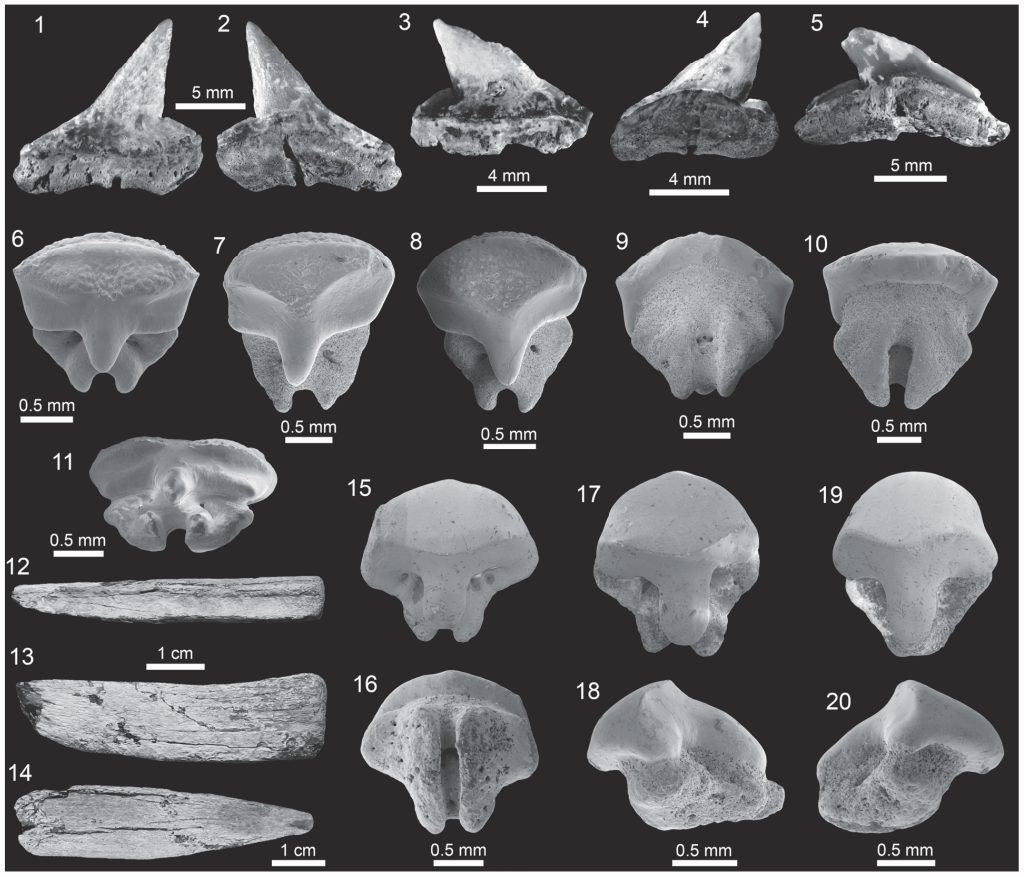

FIGURE 8. Carcharhiniformes and Rajiformes of the Cantaure Formation. 1-5. *Sphyrna* cf. †*S. laevissima* (1-3, 5: AMU-CURS-964 and 4: AMU-CURS-963). 6-11. *Rhynchobatus* sp. (6, 9: AMU-CURS-968; 7-8, 10: AMU-CURS-969 and 11: AMU-CURS-970). 12-20. *Pristis* sp. (rostral denticle 12-14: AMU-CURS-242; buccal teeth 15-20: AMU-CURS-967). Jaw position: upper (1-2) and indet. (3-11, 15-20). View: labial (1, 3), lingual (2, 4-5, 11), occlusal (6-8, 15, 17, 19), profile (18, 20), basal (9-10, 16), posterior (12) and dorsal (13-14).

Rajiformes Berg, 1937. This group of batoids is represented by two families, two genera and two species (Figure 2). Concerning Rhynchobatidae Garman, 1913, we report indeterminate teeth of *Rhynchobatus* Müller and Henle 1837 (Figure 8.6-8.11; Appendix 1, 4), resembling previously figured isolated teeth of *Rhynchobatus* from the late Miocene of Costa Rica, Panama and Venezuela (Laurito, 1999; Pimiento et al., 2013b; Carrillo-Briceño et al., 2015b). We refrain from taxonomic identification at the species level of the Cantaure *Rhynchobatus*, because the range of dental variation in extant species is unknown, and little is known about fossil species from the Americas. The Pristidae Bonaparte, 1838 is represented by a few specimens of oral teeth and rostral denticles of *Pristis* Linck, 1790 (Figure 8.12-8.20, Appendix 1, 4). As noted by Carrillo-Briceño et al. (2015b), *Pristis* rostral denticles are not diagnostic at species level, while isolated oral teeth are somewhat difficult to identify, because those of extant species are poorly known and are morphologically diverse.

Myliobatiformes Compagno, 1973. This group is represented by four families, eight genera and 11 species, being thus the second most abundant and diverse order from the Cantaure assemblage (Figure 2; Table 1; Appendix 1, 4). The Dasyatidae Jordan, 1888, is represented by three genera and four

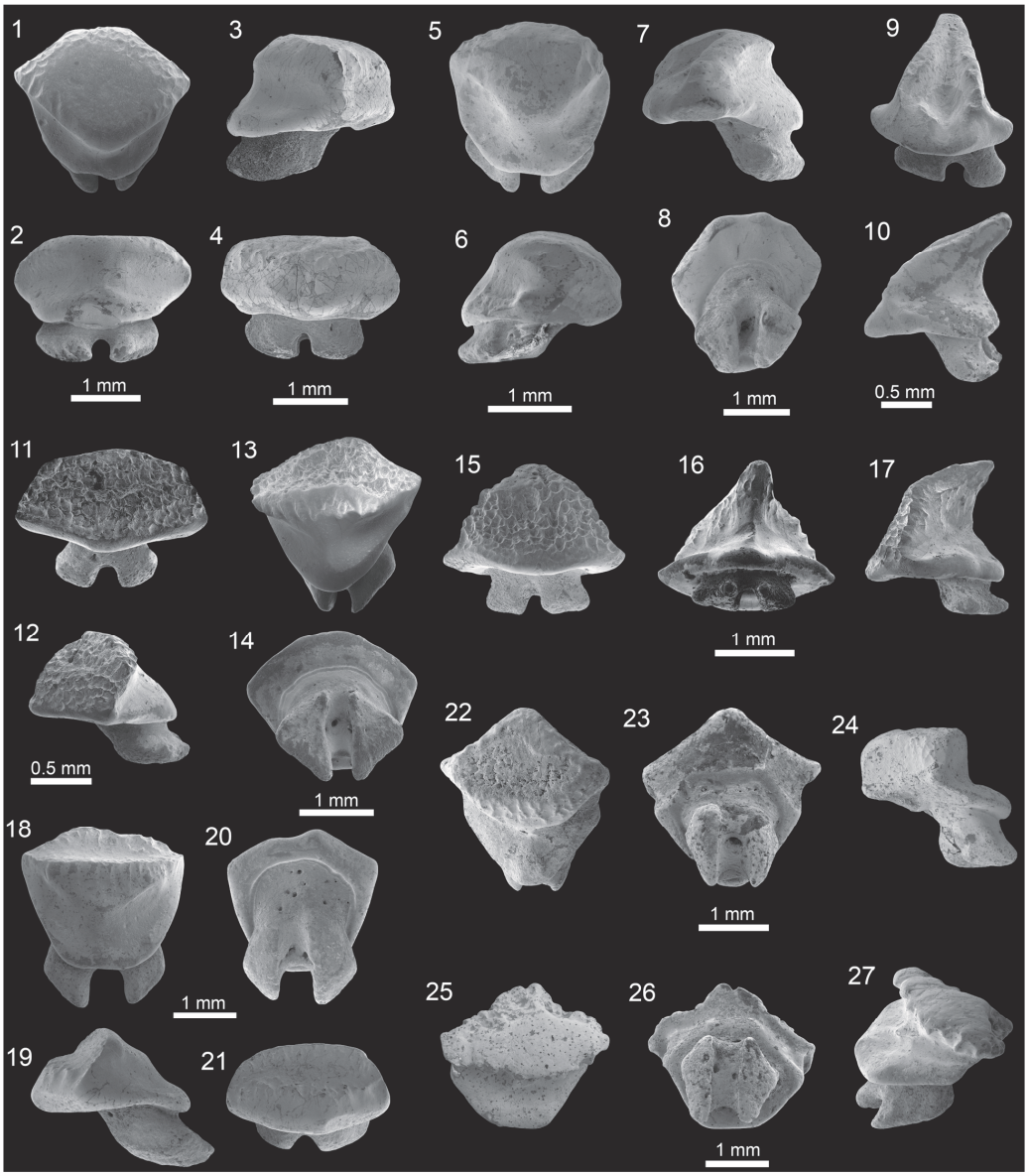

FIGURE 9. Myliobatiformes of the Cantaure Formation. 1-10. *Dasyatis* sp. (1-2, 7-8: AMU-CURS-930; 3-4: AMU-CURS-932; 5-6: AMU-CURS-933 and 9-10: AMU-CURS-931). 11-17. cf. *Pteroplatytrygon* sp. (AMU-CURS-926). 18-21. cf. *Taeniurops* sp. (AMU-CURS-925). 22-27. Dasyatidae indet. (22-24: AMU-CURS-936 and 25-27: AMU-CURS-937). Jaw position: indet. (1-27). View: labial (4, 9, 11, 15, 21), lingual (2, 16), occlusal (1, 5, 13, 18, 22, 25), profile (3, 6-7, 10, 12, 17, 19, 24, 27) and basal (8, 14, 20, 23, 26).

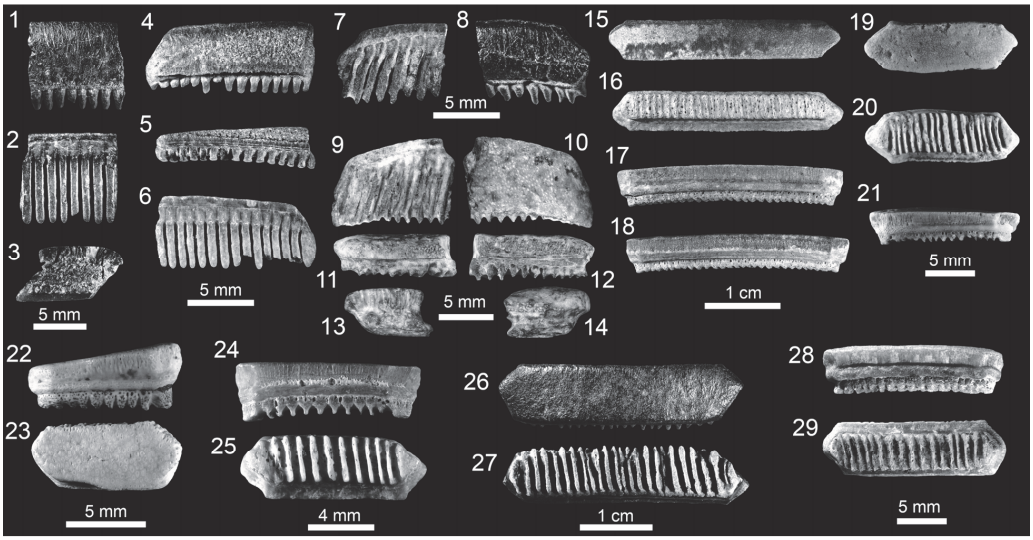

FIGURE 10. Myliobatiformes of the Cantaure Formation. 1-3. *Aetobatus* sp. (1-3: AMU-CURS-716). 4-14. *Aetomylaeus* sp. (AMU-CURS-750). 15-29. *Rhinoptera* sp. (15-18: AMU-CURS-979; 19-21, 22-23, 24-25, 28-29: AMU-CURS-977 and 26-27: AMU-CURS-981). Jaw position: indet. (1-29). View: labial (11, 18), lingual (5, 12, 17, 21-22, 24, 28), occlusal (1, 4, 8, 10, 15, 19, 23, 26), profile (3, 13-14) and basal (2, 6, 7, 9, 16, 20, 25, 27, 29).

species, and the Myliobatidae Bonaparte, 1838 and Rhinopteridae Jordan and Evermann, 1896 by one genus and one species each (Figure 2; Table 1). Due to the small number of specimens and the lack of diagnostic characters, teeth referred to *Dasyatis* Rafinesque, 1810 (Figure 9.1-9.10), cf. *Pteroplatytrygon* Fowler, 1910 (Figure 9.11-9.17), cf. *Taeniurops* Garman, 1913 (Figure 9.18-9.21), and Dasyatidae indet. (Figure 9.22-9.27), cannot be assigned to species. As noted by Carrillo-Briceño et al. (2015b), there is very little known available about the morphological diversity of dental patterns in extant and fossil Dasyatidae from the Americas.

Teeth referred to *Aetobatus* Blainville, 1816 (Figure 10.1-10.3), and *Aetomylaeus* Garman, 1913 (Figure 10.4-10.14), are fragmented and incomplete; but preserve diagnostic characters that made their generic identification possible. Teeth of *Rhinoptera* Cuvier, 1829 (Figure 10.15-10.29) are common in all localities (especially at locality 2), being the third most abundant species of the assemblage (Appendix 1, 4). Previous work on the Cantaure Formation has reported the presence of *Myliobatis* Cuvier, 1816 teeth (Aguilera and Rodrigues de Aguilera, 2004; Aguilera and Lundberg, 2010; Aguilera, 2010). However, our revision of fossils led to the identification of isolated medial and lateral teeth, which exhibit the typical imbrication pattern and morphology of *Rhinoptera*. Mobulidae Gill, 1893 is represented by two genera and four species (Figure 2; Table 1; Appendix1, 4). The mobulids †*Mobula fragilis* Cappetta, 1970 (Figure 11.1-11.11), *Mobula* cf. †*M. loupianensis* Cappetta, 1970 (Figure 11.12-11.18) and *Mobula* sp. (Figure 11.19-11.23) are scarce (Appendix1, 4), and their teeth have been recovered from localities 1 and 2 only. One tooth of †*Plinthicus stenodon* Cope, 1869 was found at locality 3.

All eroded, broken and non-diagnostic caudal spines (Figure 12.1-12.6) are referred to Myliobatiformes indet. In addition, specimens referred to Chondrichthyes indet. correspond to fragmented and non-diagnostic vertebrae (Figure 12.7-12.8).

Elasmobranch Paleobathymetric Analysis

The Cantaure elasmobranch fauna is characterized by a predominance of benthopelagic sharks and rays, the extant relatives of which inhabit diverse environments and have diverse bathymetric preferences, especially in neritic/epipelagic environments (Appendix 3). Our paleobathymetric analysis indicates that the most probable deposition depth for the Cantaure assemblage is the 0 to 50 m interval, followed by the 50 to 100 m interval as the second most probable (Figure 13). This sug-

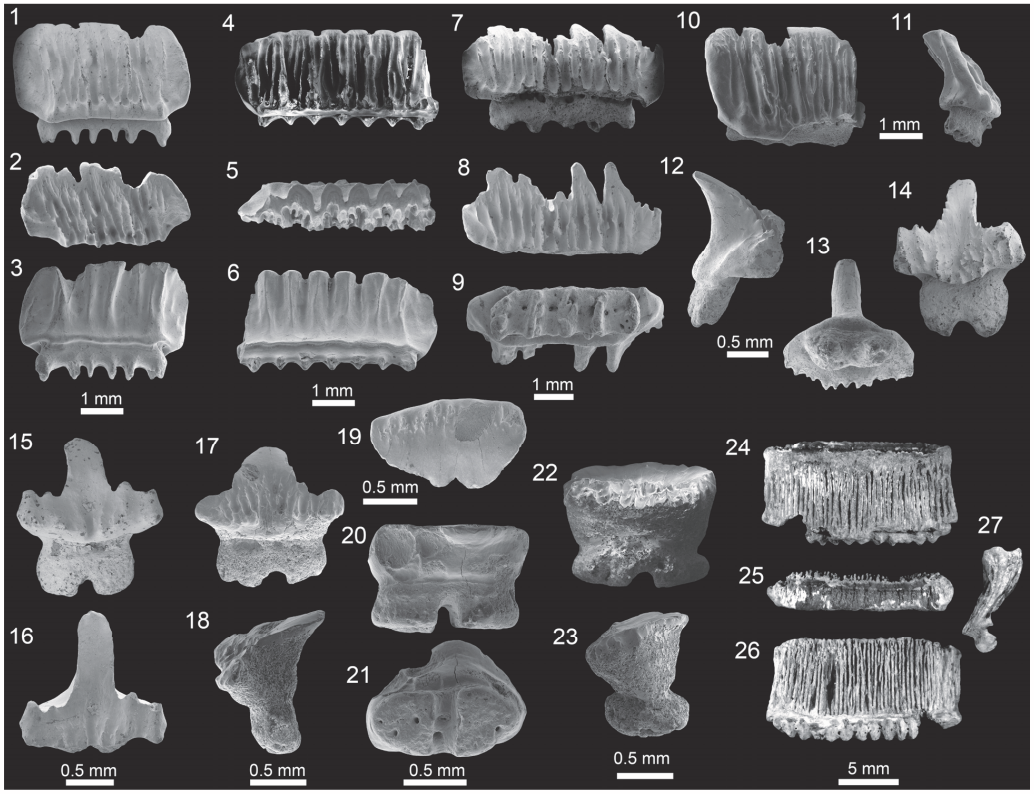

FIGURE 11. Mobulids of the Cantaure Formation. 1-11. †*Mobula fragilis* (1-3, 10-11: AMU-CURS-947; 4-6: AMU-CURS-948 and 7-9: AMU-CURS-949). 12-18. *Mobula* cf. †*M. loupianensis* (AMU-CURS-946). 19-23. *Mobula* sp. (AMU-CURS-927). 24-27. †*Plinthicus stenodon* (AMU-CURS-715). Jaw position: indet. (1-27). View: labial (1, 4, 7, 10, 14-15, 17, 22, 24), lingual (3, 6, 20, 26), occlusal (2, 5, 8, 16, 19, 25), profile (11-12, 18, 23, 27) and basal (9, 13, 21).

gests that the Cantaure Formation was deposited in an inner-middle shelf environment. The presence of *Nebrius* sp., *Carcharhinus* cf. *C. limbatus*, *C. perezi*, *Isogomphodon acuarius*, *Negaprion eurybathrodon*, *Rhynchobatus* sp. and *Rhinoptera* sp. support this hypothesis, due to the fact that their extant representatives inhabit waters shallower than those of middle shelf environments (Appendix 3). Other taxa recognized in the first and second most probable depth intervals (Figure 13) include Alopiidae, Carcharhinidae, Sphyrnidae, Rinchobatidae, Pristidae, Dasyatidae, Myliobatidae and Mobulidae, whose extant representatives are associated with coastal environments. However, it is important to keep in mind that some of those species also have a wide vertical distributional range (Appendix 3), or are even able to move along significant distances over oceanic basins (Compagno, 1984b; Compagno et al., 2005; Voigt and Weber, 2011; Froese and Pauly, 2015).

Dietary Preferences of the Cantaure Elasmobranchs

The dietary composition of the elasmobranch assemblage from the Cantaure Formation can be represented by five food categories, from filter feeders to benthic-pelagic predators (Figure 14; Appendix 3). In this assemblage the most abundant feeder group is that of the piscivorous, representing 49% of the total species count (Figure 14; Appendix 3). We have included in this group the pelagic lamnid *Paratodus benedenii* (Cappetta, 1987, Kent and Powell, 1999) and the carcharhinid *Physogaleus contortus*, extinct species with a cut-

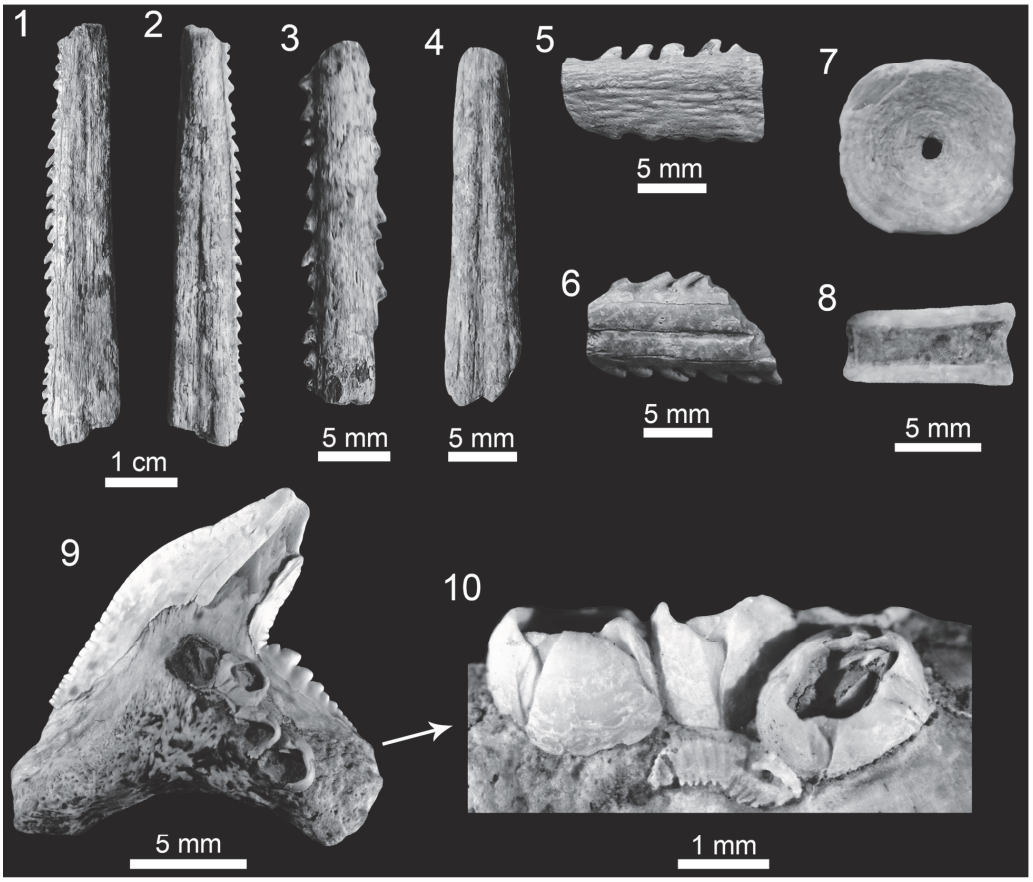

FIGURE 12. Myliobatiformes and other chondrichthyans of the Cantaure Formation. 1-6. Myliobatiformes indet. (AMU-CURS-507). 7-8. vertebra of chondrichthyan Indet. (AMU-CURS-928). 9-10. tooth of †*Galeocerdo aduncus* in association with barnacles of the family Balanidae (AMU-CURS-720). Jaw position: indet. (9). View: lingual (9), dorsal (1, 4, 5-6), ventral (2-3) and indet. (7-8).

ting-clutching dental type that could suggest a fish-based diet. The durophagous/cancritrophic (mollusk, crustacean, coral feeders) group is the second most abundant, corresponding to 30% of the species in the Cantaure assemblage, with a predominance of Myliobatiformes and Rajiformes (Figure 14; Appendix 3). In this group the most abundant taxon is *Rhinoptera* sp., living species of which are opportunistic/generalists consuming mainly mollusks. The filter feeder group (Figure 14) is represented in the Cantaure assemblage only by mobulids (Table 1; Appendix 1, 4), whose living counterparts are characterized by a diet based mainly on planktonic microorganisms (Klimley, 2013). One of its representatives is the extinct mobulid *Plinthicus stenodon*, whose fragile teeth also suggest a possible filter diet of soft prey (Cappetta, 2012). In the eurytrophic/sarcophagous group (diverse food source: fishes, reptiles, birds, mammals, etc.) (Figure 14), we have included large sharks with a broad habitat preference. Those species include *Carcharocles megalodon*, *Galeocerdo aduncus* and *G. mayumbensis*, which could have had the role of apex predators. In reference to the teuthitrophic group, it is represented only by *Alopias* cf. *A. vulpinus*, whose living counterpart has a higher preference for cephalopods (Cortés, 1999; Appendix 3).

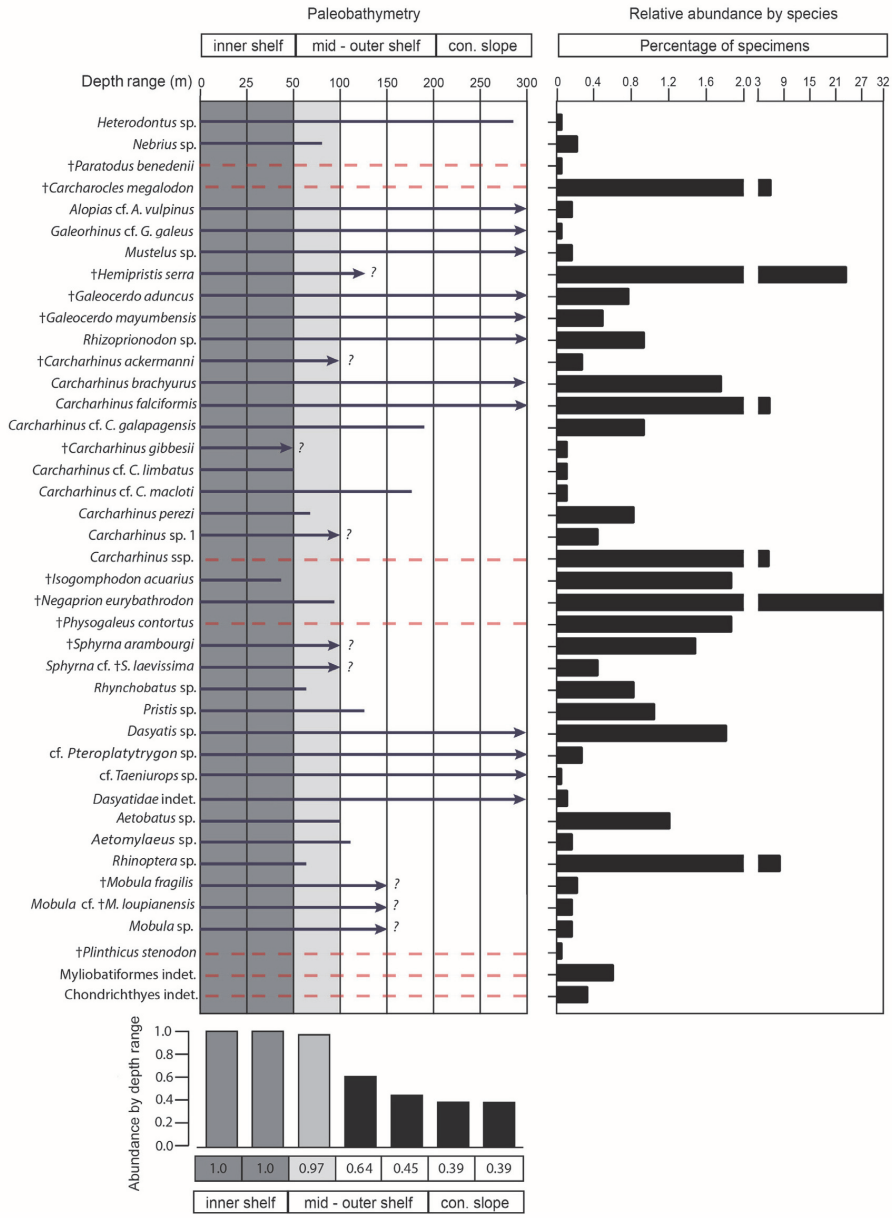

FIGURE 13. Bathymetric ranges estimated for Cantaure Formation taxa and their relative abundance. Arrows indicate that the bathymetric range is greater; question mark symbol indicates uncertainty about the extent of the range. A dashed red line indicates that there is no information for the taxa. The gray shadow indicates the more probably depth range for this assemblage. In the relative abundance graphic the y-axis is shortened between 2 and 3 to improve the values visualization; note the greater abundance of shallow water taxa. The extinct species including *P. benedenii*, *C. megalodon*, *P. contortus,* and *P. stenodon*, and taxa without clear identification, including *Carcharhinus* spp., Carcharhinidae indet., Myliobatiformes indet. and Chondrichthyes indet., were removed from the analysis.

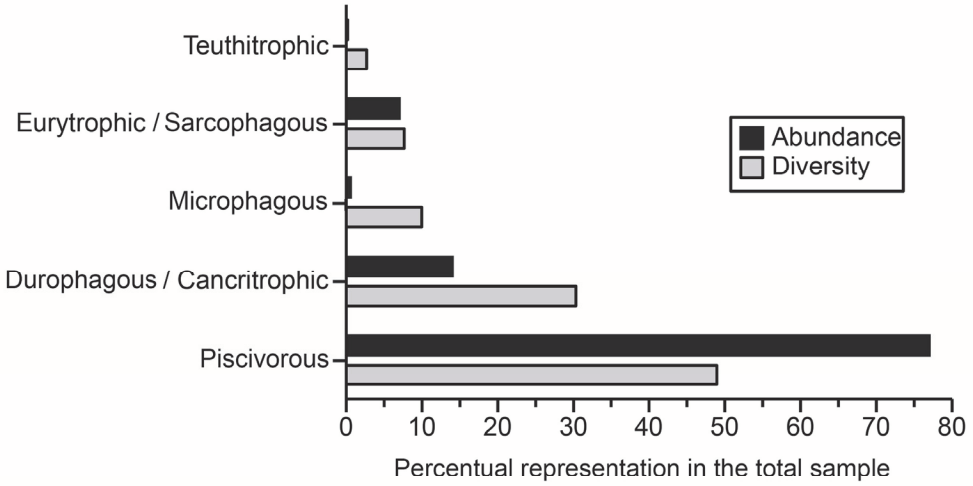

FIGURE 14. Dietary preference composition of the elasmobranchs from the Cantaure Formation. Percentages do not include *Carcharhinus* spp., Myliobatiformes indet. and Chondrichthyes indet.

DISCUSSION

Paleodiversity Significance

Forty-four percent of the Cantaure elasmobranch assemblage consists of genera or species with living representatives in Tropical America (Compagno, 1984a, 1984b; Compagno et al., 2005; Voigt and Weber, 2011). Five genera and 15 species present are extinct (Table 1). *Nebrius* sp., *Carcharhinus* cf. *C. macloti*, and *Rhynchobatus* sp., are present in our fossil sample and are currently extinct in the Caribbean, but have living counterparts in the eastern Atlantic and Indo-West Pacific (Compagno et al., 2005; Froese and Pauly, 2015). Their fossil record confirms that these taxa became extinct in the Caribbean, Western Atlantic and Eastern Pacific, possibly as a consequence of ecological competition with other species or environmental changes during the final stage of the CAS (e.g., Coates and Stallard, 2013).

The galeomorphs *Paratodus benedenii*, *Galeocerdo mayumbensis*, *C. brachyurus*, *Carcharhinus* cf. *C. galapagensis*, *C. gibbesii*, *Carcharhinus* cf. *C. macloti*, *Isogomphodon acuarius*, *Physogaleus contortus*, *Sphyrna arambourgi*, *Sphyrna* cf. *S. laevissima*, and the batoids cf. *Pteroplatytrygon* sp., cf. *Taeniurops* sp., *Mobula fragilis* and *Mobula* cf. *M. loupianensis* are reported for the first time from Neogene Venezuelan deposits. *Paratodus benedenii*, *Carcharhinus* cf. *C. galapagensis*, *Carcharhinus* cf. *C. macloti*, cf. *Pteroplatytrygon* sp, *Taeniurops* sp., *Mobula fragilis* and *Mobula* cf. *M. loupianensis* are new records for the Neogene of Tropical America. With the exception of the records mentioned above from Tropical America, the fossil record of most elasmobranch taxa from the Cantaure Formation have been found in other Neogene marine deposits of the Americas and are summarized in Kruckow and Thies (1990), Laurito (1999), Purdy et al. (2001), Aguilera et al. (2011), González-Rodríguez et al. (2013) and Carrillo-Briceño et al. (2014, 2015a, 2016).

Early Neogene marine elasmobranch assemblages known from the Americas are summarized in Figure 15 and include North America (Purdy et al., 2001; Visaggi and Godfrey, 2010), Southern South America (Suarez et al., 2006; Cione et al., 2011) and Tropical America (Leriche, 1938; Casier, 1966; MacPhee et al., 2003; Alván et al., 2006; Portell et al., 2008; Costa et al., 2009; Aguilera and Lundberg, 2010; Pimiento et al., 2013b, Laurito et al., 2014; Carrillo-Briceño et al., 2016). From these assemblages the Uitpa Formation (Colombia) has been referred to the Aquitanian (Carrillo-Briceño et al., 2016), while the Calvert and Pungo River formations in North America (Purdy et al., 2001; Visaggi and Godfrey, 2010) and the Cantaure (in this work) and Castillo (Rincón et al., 2014) formations in Venezuela, have been referred to the Burdiga-

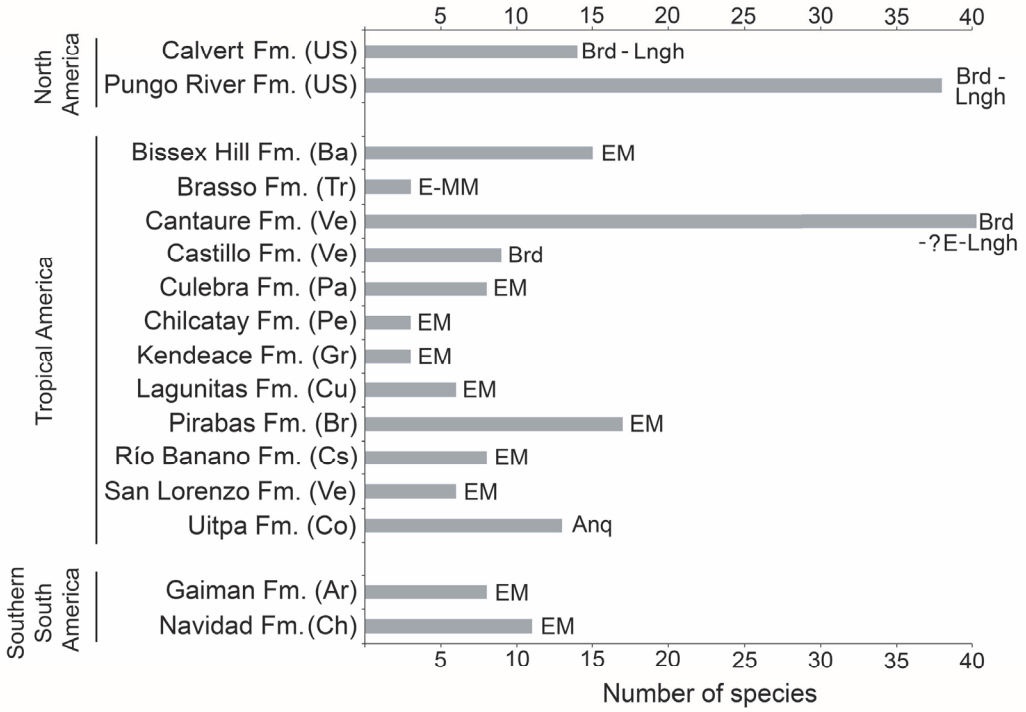

FIGURE 15. Early Neogene chondrichthyan diversity in the Americas. Tropical America: Barbados (Ba), Brazil (Br), Colombia (Co), Costa Rica (Cs), Cuba (Cu), The Grenadines (Gr), Panamá (Pa), Perú (Pu), Trinidad (Tr) and Venezuela (Ve). North America: United States of America (US). Southern South America: Argentina (Ar) and Chile (Ch). Aquitanian (Anq), Burdigalian (Brd), Langhian (Lngh); early Miocene without differentiation (EM), early-Middle Miocene (E-MM). Formation(Fm.), early (E). Note: to references see "Paleodiversity significance" (see Discusion).

lian. The remaining formations (Figure 15) have been assigned to an unresolved early Miocene age. The Pungo River (~38 spp.) and Cantaure (39 spp.) assemblages preserve the most diverse elasmobranch faunas known from early Miocene of the Americas.

The late Burdigalian age (16.5±0.4 Ma.) of the Cantaure Formation based on Sr isotopes from corals from locality 2 of Griffiths et al. (2013) (Figure 1.2), suggests that all specimens found in localities 1 and 2 could be coetaneous or older than 16.5±0.4 Ma. The poorly known stratigraphic position of localities 3 and 4, in reference to localities 1 and 2 (different vertical strata along the Cantaure section or horizontal variation of localities 1 and 2), does not permit an accurate age estimation for them, but their stratigraphic position (underlying the limestones interpreted as post-Cantaure sedimentation; Jung, 1965; Hunter and Bartok, 1974), suggests that these localities (3 and 4) are close to the top section of the Cantaure Formation. A Burdigalian age (Griffiths et al., 2013), or even that of a Burdigalian-Langhian boundary for the upper section of the Cantaure Formation (assuming that the biozones N7-8 and NN4-5 represent the lower to middle Miocene transition), would extend the stratigraphic range of two galeomorphs and of a batoid found in this assemblage. Fossils of *Carcharhinus* cf. *C. galapagensis*, from the Cantaure Formation, represent the oldest record for this species. It was previously known from the late Miocene of Mexico (González-Rodríguez et al., 2013). The same applies to *Carcharhinus gibbesii*, the youngest record was reported by Carrillo-Briceño et al. (2016) as the Aquitanian of Colombia. In reference to the batoid cf. *Pteroplatytrygon* sp., its record from the Cantaure Formation could be the oldest known to this stingray species.

The presence of *Carcharocles megalodon* in Burdigalian sediments of the Cantaure Formation (in at least localities 1 and 2) confirms the presence of this species during late early Miocene. It has been generally accepted that the record of *Carcharocles chubutensis* spans from the early to the middle Miocene, whereas *Carcharocles megalodon* spans from the middle Miocene to the late Pliocene (Pimiento and Clements, 2014; Pimiento and Balk, 2015). However, other authors have suggested that *C. megalodon* also occurs in the Burdigalian of Europe and North America (Leriche, 1938; Purdy et al., 2001; Visaggi and Godfrey, 2010; Reinecke et al., 2011). According to Leriche (1938), the two *C. megalodon* specimens he collected (Leriche, 1938, Planche III, Figures 5-6) in southern Mexico (Tabasco and Isthmus of Tehuantepec) came from early Miocene strata and are similar to teeth he previously collected in the Burdigalian of Europe. Another early Miocene unpublished occurrence of *C. megalodon* from Tropical America is from the late Burdigalian section (~16.2 Ma.) of the Castilletes Formation at North East Colombia (under study by JDCB). The specimens of *C. megalodon* from the Cantaure sequence have been found in all four localities studied here (Figure 1, Appendix 1), but with a greater abundance in localities 2 and 3 (Appendix 1). The presence of *C. megalodon* tooth (UNEFM-PF-322) at least 6-10 m deep in the artisan well (Figure 1.2) could suggest an older age than the 16.5±0.4 Ma for the species. More detailed information about the American and worldwide Neogene stratigraphic range of the remaining elasmobranch taxa recovered from the Cantaure Formation (Table 1) can be found in Kruckow and Thies (1990), Cicimurri and Knight (2009), Reinecke et al. (2011), Bor et al. (2012), Adnet et al. (2012), Cappetta, (2012), Pimiento et al. (2013b), and Carrillo-Briceño et al. (2014, 2015a, 2016).

Furthermore, it is important to note that the elasmobranch fauna from the Cantaure Formation shows a clear differentiation in paleodiversity amongst the four localities studied here (Appendix 1, 4). As is shown in Appendix 4.2, localities 1 and 2 (Figure 1) have a higher diversity than those of localities 3 and 4, a fact that could be attributable to: 1) less intensive sieving and sampling of the localities 3 and 4 (see Material and Methods section) or 2) different lithologic, taphonomic and preservational conditions. Future, more accurate dating of the deposits could offer new insights into the age of the Cantaure deposits, and especially of the sections located south of Barbasco Creek.

Paleoenvironment and Paleoecology

On the basis of planktonic foraminifera, calcareous nannofossils and mollusks, it has been proposed that the Cantaure Formation was deposited in a shallow, coastal tropical marine environment, with clear waters and normal salinity (Jung, 1965; Díaz de Gamero, 1974; Rey, 1996; Landau et al., in press). A conspicuous absence of typical herbivore gastropods suggests that sea-grass habitats were probably not represented in this environment (Landau et al., in press). The teleostean assemblage reported by Nolf and Aguilera (1998) reflects a shallow environment with a water depth of less than 50 m. The crustacean assemblage (Aguilera et al., 2010) is also suggestive of inner-shelf environments. The barnacle epifauna attached to a shark tooth AMU-CURS-720 (Figure 12.9-12.10) further indicates that the Cantaure Formation was deposited in a shallow marine environment, as barnacles live either in intertidal (26%) or sublittoral areas of ≤100 m (73%) (Doyle et al., 1996). Our bathymetric analysis of the Cantaure Formation, suggesting most likely an estimated deep interval depth between 0 to 50 m (Figure 13), supports the assumption of an inner-middle shelf environment (Figure 16). Additional support to this estimation is derived from the presence of the benthopelagic sharks *Nebrius* sp., *Carcharhinus* cf. *C. limbatus*, *C. perezi* and *Isogomphodon acuarius*, whose extant representatives usually prefer waters shallower than 40 m deep (Appendix 3). As shown in Figure 13, many of the benthopelagic and pelagic elasmobranch taxa of the Cantaure fauna have extant representatives associated with coastal environments, but can also occur in adjacent deep waters (Appendix 3), and even move significant distances over oceanic basins, suggesting a wide environmental range (Compagno et al., 2005; Voigt and Weber, 2011).

The Cantaure sequence rests on metamorphic and igneous rocks that were above water level during early Miocene (Gonzalez de Juana et al., 1980; Macellari, 1995). During the Cantaure sedimentation, these positive reliefs played the role of islands or archipelagos, as illustrated in the paleogeographic reconstruction of the Falcon Basin by Gonzalez de Juana et al. (1980) and Macellari (1995). According to Landau et al. (in press), 47.8% of the gastropod species (188 spp.) in the Cantaure Formation are exclusive, representing a very high level of endemism. This species endemism could support the hypothesis of an isolated, insular mollusk-community in the northern part of the Falcon Basin during early Miocene. However,

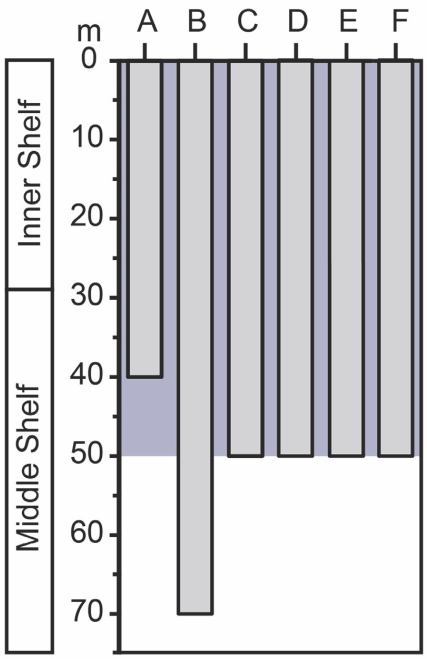

FIGURE 16. Paleobathymetric interpretation of the Cantaure Formation using several proxies. A, Foraminifera (Díaz de Gamero, 1974), B, corals (Griffiths et al., 2013), C, mollusks (Jung, 1965; Landau et al., in press), D, crustaceans (Aguilera et al., 2010), E, sharks (this study), F, teleosteans (Nolf and Aguilera, 1998, Aguilera and Rodrigues de Aguilera, 2001).

expanded knowledge of their localities will certainly lower that estimate. The Cantaure gastropod assemblage also has a small freshwater component, corresponding to typical species of late Oligocene early Middle Miocene NW South-American inland freshwater faunas (Landau et al. in press). This is likely suggestive of insular areas allowing the existence of terrestrial faunas. In addition, the diverse teleostean fauna from the Cantaure Formation, with more than 65 species (Nolf and Aguilera, 1998; Aguilera, 2010; Aguilera and Lundberg, 2010), suggests a high-productivity environment associated with a coastal upwelling (Aguilera and Rodrigues de Aguilera, 2004).

Although it is difficult to approach the precise ecological role that the Cantaure elasmobranch fauna played in this ancient marine environment, we can speculate about trophic interactions using the dietary (nutrition mode) categorization of taxa in the assemblage (Figure 14). The Cantaure assemblage is dominated by piscivorous shark species (Figure 14, Appendix, 3). This could be related to the diverse teleostean fauna of the Cantaure Formation (Nolf and Aguilera, 1998; Aguilera, 2010; Aguilera and Lundberg, 2010), whose remains (mainly otoliths) are extremely abundant, with approximately more than 60 specimens per 10 kg of sifted matrix (OAA and JDCB pers. obs.). The durophagous/cancritrophic feeders represent the second most abundant elasmobranch group in the assemblage (Figure 14, Appendix 3). Their potential benthonic prey includes some 445 mollusks species (Jackson et al., 1999; Landau et al., in press) and more than 20 crustacean species (Aguilera et al., 2010) and must have offered wide feeding opportunities. Durophagous rays with capacity to triturate hard shells were abundant in the Cantaure fauna (e.g., *Rhinoptera* sp. being the third most abundant species of the assemblage, Appendix 1, 3). The presence of mobulids (Table 1, Appendix 1, 4), whose living counterparts are characterized by a diet based mainly on planktonic microorganisms (Klimley, 2013), support the assumption of a high-productive environment associated to a coastal upwelling (Aguilera and Rodrigues de Aguilera, 2004).

A few large sharks from the Cantaure assemblage such as *Carcharocles megalodon*, *Galeocerdo aduncus* and *G. mayumbensis*, could have alternatively occupied different environments and fed on various resources, such as teleosteans, chondrichthyans, reptiles, birds and mammals. In extant marine communities many sharks are perceived as apex predators, occupying the same trophic level with marine mammals (Klimley, 2013). In the Cantaure fauna such large sharks (*C. megalodon*, *G. aduncus* and *G. mayumbensis*), together with a medium-sized odontocete (?Squalodelphinidae) (Cozzuol and Aguilera, 2008; likely occupied the apex predator role. Moreover, cetacean (squalodontids) and sirenid (dugongids) skeletal remains found in the Cantaure Formation exhibit shark bite marks, suggesting that these mammals also were prey (Cozzuol and Aguilera, 2008). A cetacean lumbar vertebra with an embedded tooth of a *Carcharocles megalodon* was reported from the early Pliocene Paraguaná Formation, in the "El Yacural" locality (Aguilera et al., 2008). Recent field work in the "El Yacural" produced new specimens that include cetacean remains (vertebra and a skull fragment; AMU-CURS-709 and 710, respectively) and a crocodilian vertebra (AMU-CURS-708).

Those specimens lack any evidence for predation. The geographic coordinates of locality 4

(Figure 1.1) are very close to the "El Yacural" locality studied by Aguilera et al. (2008), with a horizontal distance of less than 200 m. Both localities are overlain stratigraphically by limestone layers on the top of the Cerro San Carlos (OAA, JDCB, GAF, pers. obs.), which have been interpreted by Jung (1965) and Hunter and Bartok (1974) as the top of the Cantaure Formation, representing the transition between the latter unit and post-Cantaure and pre-Pliocene sedimentation. We tentatively suggest that the vertebra with an embedded *Carcharocles megalodon* tooth could belong to the Cantaure Formation and not to the early Pliocene Paraguaná Formation (Aguilera et al., 2008). As previously mentioned, the Cantaure Formation is a complex sequence that needs a new detailed stratigraphic redescription, which could offer new geological information. The sections located at the south of the Barbasco Creek are of particular relevance for future research. In addition, the crocodilian vertebra (AMU-CURS-708) and the small eroded turtle-shell fragments, although not offering useful information for taxonomical classification, verify the presence of at least two reptiles in this ancient high-productive marine environment of the Cantaure Formation.

CONCLUSIONS

The elasmobranch fauna from the Cantaure Formation, containing 39 species, is characterized by a predominance of benthopelagic sharks with piscivorous feeding preferences, followed by durophagous/cancritrophic feeders. The elasmobranch habitat preferences and paleobathymetric analyses support the hypothesis that the Cantaure Formation was deposited in a high productivity, inner-middle shelf environment, around positive reliefs (island/archipelago), in the northern part of Falcon Basin during early-?middle Miocene. This shark and ray fauna, is one of most diverse assemblages from early Neogene of the Americas, and contains many forms now extinct in the Caribbean, but present in the eastern Atlantic and western Pacific. Crocodile and turtle remains are also preserved in the Cantaure Formation.

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APPENDIX 1.

Elasmobranchii of the Cantaure Formation and their record per localities, jaw position and tooth measurements. Abbreviations: number of specimens (N°), total number of specimens (N° T) and indeterminate (indet.).

Taxon	Localities									Jaw position			Teeth measurements (mm)		
	1	N°	2	N°	3	N°	4	N°	N° T	Upper	Lower	indet.	Height	Width	Length
Heterodontus sp.	—	—	X	1	—	—	—	—	1	—	—	1	?	?	?
Nebrius sp.	X	3	X	1	—	—	—	—	4	—	—	4	2 to 11	3 to 7	—
†*Paratodus benedenii*	—	—	X	1	—	—	—	—	1	1?	—	—	32	?	—
†*Carcharocles megalodon*	X	1	X	18	X	80	X	7	106	50	31	25	23 to 127	23 to ~ 66	—
Alopias cf. *Alopias vulpinus*	X	1	X	1	X	1	—	—	3	2	—	1	9 to 11	10 to 11	—
Galeorhinus cf. *G. galeus*	X	1	—	—	—	—	—	—	1	—	—	1	2.5	5	—
Mustelus sp.	—	—	X	3	—	—	—	—	3	—	—	3	< 3	< 3	< 3
†*Hemipristis serra*	X	2	X	182	X	195	X	46	425	230	70	125	5 to 32	4.5 to 35	—
†*Galeocerdo aduncus*	X	1	X	13	—	—	—	—	14	—	—	14	11 to 18	16 to 24	—
†*Galeocerdo mayumbensis*	—	—	X	8	X	1	—	—	9	—	—	9	12 to 22	20 to 25.5	—
Rhizoprionodon sp.	X	3	X	14	—	—	—	—	17	4	6	7	2 to 3.8	2.2 to 4	—
†*Carcharhinus ackermannii*	X	5	—	—	—	—	—	—	5	3	2	—	11 to 18.2	12.7 to 20	—
Carcharhinus brachyurus	—	—	X	32	—	—	—	—	32	29	3	—	8 to 14	8 to 16.1	—
Carcharhinus falciformis	—	—	X	85	—	—	X	17	102	96	6	—	3 to 17	3 to 15.2	—
Carcharhinus cf. *C. galapagensis*	—	—	—	—	X	17	—	—	17	17	—	—	12 to 17.5	13 to 16	—
†*Carcharhinus gibbesii*	—	—	X	2	—	—	—	—	2	2	—	—	9 to 9.9	7.8 to 8	—
Carcharhinus cf. *C. limbatus*	X	2	—	—	—	—	—	—	2	2	—	—	5 to 9	6.5 to 11	—
Carcharhinus cf. *C. macloti*	—	—	X	2	—	—	—	—	2	2	—	—	3.4 to 6.3	4 to 6.7	—
Carcharhinus perezi	X	11	X	3	X	1	—	—	15	15	—	—	4 to 8	5 to 13	—
Carcharhinus sp. 1	X	8	—	—	—	—	—	—	8	8	—	—	2 to 4.5	3.2 to 6	—
Carcharhinus spp.	X	21	X	50	X	17	X	10	98	40	52	6	5 to 15	4 to 14	—
†*Isogomphodon acuarius*	X	8	X	26	—	—	—	—	34	18	16	—	3 to 10.1	3.1 to 9.5	—
†*Negaprion eurybathrodon*	X	13	X	101	X	437	X	35	586	280	306	—	6 to 19	6 to 22	—
†*Physogaleus contortus*	—	—	X	30	X	3	X	1	34	—	—	34	10 to 19	19 to 19	—
Carcharhinidae indet.	X	2	X	8	—	—	—	—	10	2	8	—	3 to 6.2	4.5 to 8	—
†*Sphyrna arambourgi*	X	14	X	13	—	—	—	—	27	14	12	1	3 to 7	4 to 7.2	—
Sphyrna cf. †*S. laevissima*	X	2	X	1	X	5	—	—	8	—	3	5	3.5 to 11.9	5.5 to 14.9	—
Rhynchobatus sp.	X	8	X	7	—	—	—	—	15	—	—	15	< 4	< 4	<4
Pristis sp.	X	5	X	13	X	1	—	—	19	—	—	19	< 3	< 3	< 3
Dasyatis sp.	X	21	X	12	—	—	—	—	33	—	—	33	< 3	< 3	< 3
cf. *Pteroplatytrygon* sp.	X	5	—	—	—	—	—	—	5	—	—	5	< 3	< 3	< 3
cf. *Taeniurops* sp.	X	1	—	—	—	—	—	—	1	—	—	1	< 3	< 3	< 3
Dasyatidae indet.	X	2	—	—	—	—	—	—	2	—	—	2	< 3	< 3	< 3
Aetobatus sp.	X	6	X	9	X	4	—	—	19	—	—	19	4.1 to 6	?	~ 4.5 to 10
Aetomylaeus sp.	X	2	X	1	—	—	—	—	3	—	—	3	?	?	?
Rhinoptera sp.	X	15	X	129	X	1	—	—	145	—	—	145	2 to 6	5 to 29	3 to 8
†*Mobula fragilis*	X	4	—	—	—	—	—	—	4	—	—	4	2.5 to 3	3.5 to > 6	1 to 1.6
Mobula cf. †*M. loupianensis*	X	3	—	—	—	—	—	—	3	—	—	3	< 2	< 2	< 2
Mobula sp.	—	—	X	3	—	—	—	—	3	—	—	3	< 2	< 2	< 2
†*Plinthicus stenodon*	—	—	—	—	X	1	—	—	1	—	—	1	8	15.5	4
Myliobatiformes indet.	—	—	X	11	—	—	—	—	11	—	—	—	?	?	?
Chondrichthyes indet.	—	—	X	6	—	—	—	—	6	—	—	—	?	?	?
Total:		170		786		764		116	: 1836						

APPENDIX 2.

Referred fossil specimens and collection numbers.

Referred fossil specimens

- *Nebrius* sp. [1 tooth (AMU-CURS-982), 1 tooth (AMU-CURS-986)].

- †*Paratodus benedenii* [1 tooth (AMU-CURS-645)].

-†*Carcharocles megalodon* [4 teeth (AMU-CURS-512), 3 teeth (AMU-CURS-513), 2 teeth (AMU-CURS-514), 2 teeth (AMU-CURS-515), 3 teeth (AMU-CURS-516), 4 teeth (AMU-CURS-517), 3 teeth (AMU-CURS-518), 1 tooth (AMU-CURS-519), 4 teeth (AMU-CURS-650), 1 tooth (AMU-CURS-996), 1 tooth (AMU-CURS-997), 1 tooth (AMU-CURS-998), 7 teeth (AMU-CURS-1034), 1 tooth (UNEFM-PF-321), 1 tooth (UNEFM-PF-322), 13 teeth (UNEFM-PF-s/n), 17 teeth (UNEFM-PF-s/n), 21 teeth (UNEFM-PF-s/n), 17 teeth (MCNC-s/n)].

-*Alopias* cf. *A. vulpinus* [1 tooth (AMU-CURS-983), 1 tooth (AMU-CURS-984), 1 tooth (AMU-CURS-985)].

-*Galeorhinus* cf. *G. galeus* [1 tooth (AMU-CURS-974)].

-*Mustelus* sp. [3 teeth (AMU-CURS-975)].

-†*Hemipristis serra* [66 teeth (AMU-CURS-502), 1 tooth (AMU-CURS-506), 6 teeth (AMU-CURS-520), 24 teeth (AMU-CURS-644), 3 teeth (AMU-CURS-712), 1 tooth (AMU-CURS-731), 1 tooth (AMU-CURS-973), 1 tooth (AMU-CURS-993), 1 tooth (AMU-CURS-994), 1 tooth (AMU-CURS-1014), 46 1 tooth (AMU-CURS-1031), 156 (UNEFM-PF-s/n), 118 teeth (UNEFM-PF-s/n).

-†*Galeocerdo aduncus* [13 teeth (AMU-CURS-647), 1 tooth (AMU-CURS-730)].

-†*Galeocerdo mayumbensis* [8 teeth (AMU-CURS-646), 1 tooth (AMU-CURS-995)].

-*Rhizoprionodon* sp. [14 teeth (AMU-CURS-959), 3 teeth (AMU-CURS-960)].

-†*Carcharhinus ackermannii* [3 teeth (AMU-CURS-713), 2 teeth (AMU-CURS-714)].

-*Carcharhinus brachyurus* [28 teeth (AMU-CURS-668), 4 teeth (AMU-CURS-990)].

-*Carcharhinus falciformis* [72 teeth (AMU-CURS-669), 6 teeth (AMU-CURS-991), 11 teeth (AMU-CURS-953), 17 teeth (AMU-CURS-1035)].

-*Carcharhinus* cf. *C. galapagensis* [17 teeth (AMU-CURS-973)].

-†*Carcharhinus gibbesii* [2 teeth (AMU-CURS-958)].

-*Carcharhinus* cf. *C. limbatus* [2 teeth (AMU-CURS-944)].

-*Carcharhinus* cf. *C. macloti* [2 teeth (AMU-CURS-957)].

-*Carcharhinus perezi* [1 tooth (AMU-CURS-954), 3 teeth (AMU-CURS-955), 11 teeth (AMU-CURS-956)].

-*Carcharhinus* sp. 1 [8 teeth (AMU-CURS-943)].

-*Carcharhinus* spp. [22 teeth (AMU-CURS-651), 26 teeth (AMU-CURS-652), 14 teeth (AMU-CURS-940), 7 teeth (AMU-CURS-941), 10 teeth (AMU-CURS-942), 7 teeth (AMU-CURS-972), 1 tooth (AMU-CURS-1015), 1 tooth (AMU-CURS-1017), 10 teeth (AMU-CURS-1085)].

-†*Isogomphodon acuarius* [8 teeth (AMU-CURS-950), 25 teeth (AMU-CURS-951), 1 tooth (AMU-CURS-952)].

-†*Negaprion eurybathrodon* [165 teeth (AMU-CURS-503), 65 teeth (AMU-CURS-504), 56 teeth (AMU-CURS-505), 1 tooth (AMU-CURS-509), 47 teeth (AMU-CURS-649), 13 teeth (AMU-CURS-987), 1 tooth (AMU-CURS-998), 52 teeth (AMU-CURS-989), 1 tooth (AMU-CURS-1013), 35 (AMU-CURS-1032), 150 teeth (UNEFM-PF-s/n)].

-†*Physogaleus contortus* [29 teeth (AMU-CURS-648), 2 teeth (AMU-CURS-992), 1 tooth (AMU-CURS-1033), 1 tooth (AMU-CURS-719), 1 tooth (AMU-CURS-720)].

APPENDIX 2 (CONTINUED).

-Carcharhinidae indet. [2 teeth (AMU-CURS-938), 8 teeth (AMU-CURS-939)].

-†*Sphyrna arambourgi* [14 teeth (AMU-CURS-961), 13 teeth (AMU-CURS-962)].

-*Sphyrna* cf. †*S. laevissima* [1 tooth (AMU-CURS-963), 5 teeth (AMU-CURS-964), 1 tooth (AMU-CURS-965)].

-*Rhynchobatus* sp. [4 teeth (AMU-CURS-653), 2 teeth (AMU-CURS-654), 3 teeth (AMU-CURS-968), 4 teeth (AMU-CURS-969), 1 tooth (AMU-CURS-970), 1 tooth (AMU-CURS-971)].

-*Pristis* sp. [7 rostral denticles and 1 rostrum fragment (AMU-CURS-242), 1 rostral denticle (AMU-CURS-717), 3 teeth (AMU-CURS-655), 1 tooth (AMU-CURS-1019), 1 tooth (AMU-CURS-966), 5 teeth (AMU-CURS-717)].

-*Dasyatis* sp. [1 tooth (AMU-CURS-657), 1 tooth (AMU-CURS-658), 12 teeth (AMU-CURS-929), 5 teeth (AMU-CURS-930), 10 teeth (AMU-CURS-931), 1 tooth (AMU-CURS-932), 1 tooth (AMU-CURS-933), 1 tooth (AMU-CURS-934), 1 tooth (AMU-CURS-935)].

- cf. *Pteroplatytrygon* sp. [5 teeth (AMU-CURS-926)].

-cf. *Taeniurops* sp. [1 tooth (AMU-CURS-925)].

-Dasyatidae indet. [1 tooth (AMU-CURS-936), 1 tooth (AMU-CURS-937)].

-*Aetobatus* sp. [1 tooth (AMU-CURS-508), 1 tooth (AMU-CURS-659), 4 teeth (AMU-CURS-663), 4 teeth (AMU-CURS-665), 6 teeth (AMU-CURS-716), 2 teeth (AMU-CURS-718), 1 tooth (AMU-CURS-729)].

-*Aetomylaeus* sp. [1 tooth (AMU-CURS-750), 2 teeth (AMU-CURS-766)].

-*Rhinoptera* sp. [80 teeth (AMU-CURS-660), 1 tooth (AMU-CURS-664), 4 teeth (AMU-CURS-977), 6 teeth (AMU-CURS-978), 28 teeth (AMU-CURS-979), 11 teeth (AMU-CURS-980), 15 teeth (AMU-CURS-981)].

-†*Mobula fragilis* [2 teeth (AMU-CURS-947), 1 tooth (AMU-CURS-948), 1 tooth (AMU-CURS-949)].

-*Mobula* cf. †*M. loupianensis* [3 teeth (AMU-CURS-946)].

-*Mobula* sp. [3 teeth (AMU-CURS-945)].

-†*Plinthicus stenodon* [1 tooth (AMU-CURS-715)].

-Myliobatiformes indet. [10 caudal spines (AMU-CURS-507), 1 tooth (AMU-CURS-510), 1 tooth (AMU-CURS-1018)].

-Chondrichthyes indet. [4 vertebrae (AMU-CURS-511), 2 denticles (AMU-CURS-656)].

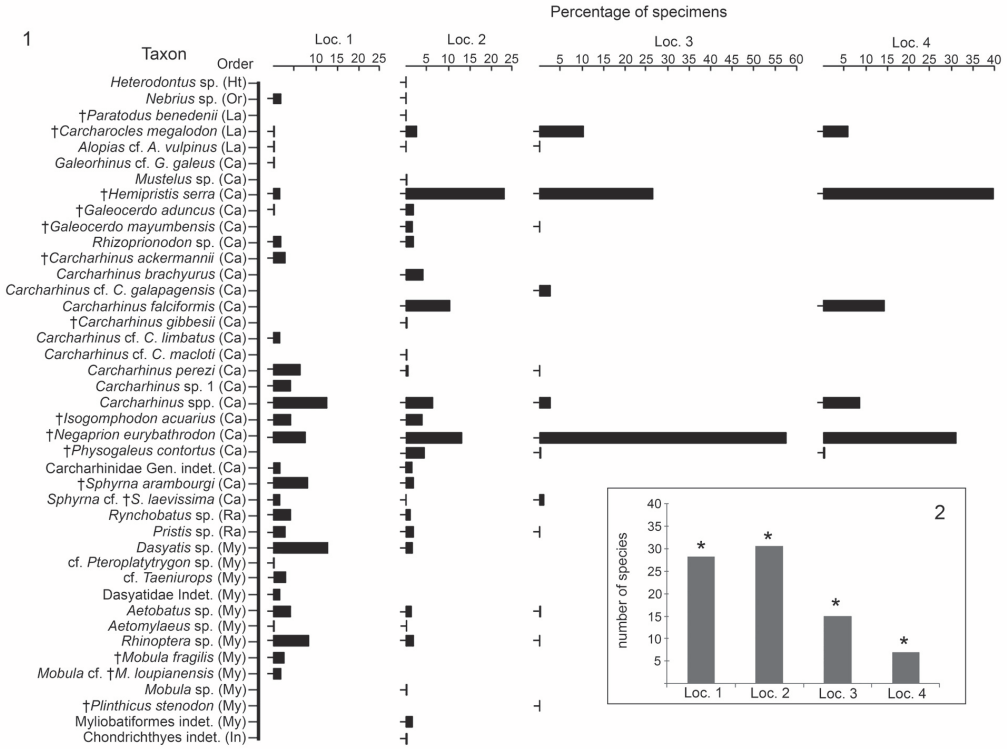
APPENDIX 3.

Bathymetric and feeding preferences of the Cantaure Formation elasmobranch taxa, based on the biology of their extant relatives. The gray shadow indicates the feeding preferences. Abbreviations: minimun (Mn), maximun (Mx) and meters (m).

Cantaure Formation taxa	Extant species	Habitat of living representatives								Feeding ecology						
										Behavior		Diet				
		Benthic	Benthopelagic	Pelagic	Neritic / Epipelagic	Bathyal / Meso-Bathypelagic	Bathymetry depth (m) Mn	Bathymetry depth (m) Mx	Comments	Filter feeders	Benthic / pelagic predators	Piscivorous	Durophagous / Cancritrophic	Teuthidrophic	Eurytrophic / Sarcophagous	Microphagous
Heterodontus sp.	*Heterodontus* spp.	X			X	X	0	280			X	X	X			
Nebrius sp.	*Nebrius ferrugineus*	X			X		1	70	usually less than 30 m		X	X	X	X		
†*Paratodus benedenii*	—			X	X	?	?	?			X	X			?	
†*Carcharocles megalodon*	—		?	X	X	?	0	?				X			X	
Alopias cf. *A. vulpinus*	*Alopias vulpinus*			X	X	X	0	550	usually less than 200 m			X		X		
Galeorhinus cf. *G. galeus*	*Galeorhinus galeus*		X		X	X	0	1100	usually 2-400 m		X	X	X	X		
Mustelus sp.	*Mustelus* spp.		X		X	X	0	900			X	X	X			
†*Hemipristis serra*	*Hemipristis elongata*		X		X		0	~ 130			X	X		?	?	
†*Galeocerdo aduncus*	*Galeocerdo cuvier*		X		X	?	0	~ 370	usually less than 150 m		X	X	X	X	X	
†*Galeocerdo mayumbensis*	*Galeocerdo cuvier*		X		X	?		~ 370	usually less than 150 m		X	X	X	X	X	
Rhizoprionodon sp.	*Rhizoprionodon* spp.		X		X		0	500	usually less than 100 m		X	X	X	X		
†*Carcharhinus ackermannii*	*Carcharhinus* spp.		?	X	X	?	0	>100?			X	X				
Carcharhinus brachyurus	*Carcharhinus brachyurus*		X		X	X	0	~ 360	usually less than 100 m		X	X		X		
Carcharhinus falciformis	*Carcharhinus falciformis*			X	X	X	0	4000	most in waters > 200 m		X	X		X		
Carcharhinus cf. *C. galapagensis*	*Carcharhinus galapagensis*		X		X		0	180			X	X				
†*Carcharhinus gibbesii*	*Carcharhinus* spp.		?	X	X	?	0	>100?			X	X		X		
Carcharhinus cf. *C. limbatus*	*Carcharhinus limbatus*		X		X		0	100	usually less than 30 m		X	X		X		
Carcharhinus cf. *C. macloti*	*Carcharhinus macloti*			X	X		0	170			X	X		X		
Carcharhinus perezi	*Carcharhinus perezi*		X		X		0	65	usually less than 30 m		X	X				
Carcharhinus sp. 1	*Carcharhinus* spp.		?	?	X	?	0	>100?				X				
Carcharhinus spp.	*Carcharhinus* spp.		X	X	X	?	0	>100?			X	?	?	?		
†*Isogomphodon acuarius*	*Isogomphodon oxyrhynchus*		X		X		0	40			X	X				
†*Negaprion eurybathrodon*	*Negaprion brevirostris*		X		X		0	92			X	X				
†*Physogaleus contortus*	—		?	X	X	?	?	?			X	X				
Carcharhinidae indet.	Carcharhinidae spp.		?	?	X	?	0	>100?			X	X				
†*Sphyrna arambourgi*	*Sphyrna* spp.		X		X	?	0	>100?			X	X				
Sphyrna cf. †*S. laevissima*	*Sphyrna zygaena*		X		X		0	>100?	usually less than 20 m		X	X				
Rhynchobatus sp.	*Rhynchobatus* spp.		X		X		0	~ 60			X	X	X			
Pristis sp.	*Pristis* spp.		X		X		0	~ 120	most in waters < 20 m		X	X	X			
Dasyatis sp.	*Dasyatis* spp.	X			X	X	0	~470	most in waters < 50 m		X	X	X			
cf. *Pteroplatytrygon sp.*	*Pteroplatytrygon violacea*	X			X	X	0	381	usually 1-100 m		X	X	X	X		
cf. *Taeniurops*	*Taeniurops* spp.	X			X	X	10	500	usually 20-60 m		X	X	X			
Dasyatidae indet.	Dasyatidae spp.	X			X	X	0	~470			X	X	X			
Aetobatus sp.	*Aetobatus* spp.		X		X		0	~ 100	usually less than 40 m		X	X	X	X		
Aetomylaeus sp.	*Aetomylaeus* spp.		X				0	110			X	X	X	X		
Rhinoptera sp.	*Rhinoptera* spp.		X		X		0	< 60	usually less than 30 m		X	X	X			
†*Mobula fragilis*	*Mobula* spp.			X	X	?	0	>200	usually less than 100 m	X						X
Mobula cf. †M. loupianensis	*Mobula* spp.			X	X	?	0	>200	usually less than 100 m	X						X
Mobula sp.	*Mobula* spp.			X	X	?	0	>200	usually less than 100 m	X						X
†*Plinthicus stenodon*	—		X		X	?	?	?		X						X
Myliobatiformes indet.	—	?	?	?	?	?	?	?		?	?					
Choudrichthyes indet.	—	?	?	?	?	?	?	?								

APPENDIX 4.

Relative abundance of elasmobranchs in the Cantaure Formation. 1. Abundance percentage per locality per taxon. 2. Total abundance per locality. Ht: Heterodontiformes; Or: Orectolobiformes; La: Lamniformes; Ca: Carcharhiniformes; Ra: Rajiformes; My: Myliobatiformes; In: Indeterminate; Loc.: locality; †: extint taxon. *: Percentage does not include *Carcharhinus* spp., Myliobatiformes indet. and Chondrichthyes indet.



CHAPTER 7

Conclusions and future perspectives

Conclusions and future perspectives

This dissertation, as a whole, with the description and publication of eleven elasmobranch assemblages from the Caribbean region (Colombia, Panama and Venezuela) and Eastern Pacific (Ecuador), plus the ongoing description of four more assemblages from the early Miocene of Colombia and Brazil (e.g. Carrillo-Briceño et al., and Aguilera et al., both in prep.), capitalizes on long-term, previous fieldwork efforts, providing new insights of the chondrichthyan paleodiversity inhabiting Tropical America during the Neogene. The new assemblages document shallow and deep-water habitats. Among the finding are 17 taxa reported for the first time for Tropical America. Fossil remains of chimaeras (Holocephali) were not found in our assemblages, being until now the record of *Chimaera* sp. from the late Miocene-Pliocene of Costa Rica (Laurito, 2008) and *Callorhinchus* cf. *C. callorhinchus* from the Pliocene of Peru (De Muizon and Devries, 1985), the only representatives of this group known from the Neogene of Tropical America. The comprehensive interpretation about habitat and biology of the living counterpart taxa of the fossil ones presented in the studied assemblages was the tool used for the understanding of the paleoecological and the paleoenvironmental conditions of these geologic units.

Previous to this contribution, knowledge about chondrichthyan assemblages of deep-water affinities from Tropical America was very limited, with only general descriptions from the late Miocene-Pliocene of Costa Rica and Venezuela (Laurito, 1999; Aguilera and Rodriguez de Aguilera, 2001). Thus the novelty in this work represented by the description of new faunas associated with deep-water affinities from Colombia (Uitpa Formation), Ecuador (Angostura Formation) and Panama (Chagres Sandstone Member of the Chagres Formation) (chapters 2-3 and 5), including the description of the new species of the frilled shark †*Chlamydoselachus landinii* sp. nov. (Figure 1A; Chapter 2).

Fossil assemblages characterized by taxa with shallow-water affinities from the Neogene of Tropical America are the most common ones referred in previous contributions (e.g. Leriche, 1938; Santos and Travassos, 1960; Santos and Salgado, 1971; Kindlimann, 1990; Kruckow and Thies, 1990; Iturralde-Vinent et al., 1996; Reis, 2005; Alván et al., 2007; Costa et al., 2009; Aguilera, 2010; Pimiento et al., 2013a, 2013b). The assemblages described in chapters 2-4 and 6, from mainly Miocene and Pliocene units of Ecuador (Onzole, Canoa and Jama formations), Panama (Rio Indio Member, Chagres Formation), and Venezuela (Cantaure, Socorro, Urumaco and Codore formations), provide new insights about neritic faunas and their associated paleoenvironments. An example constitute the assemblages from Ecuador (Onzole, Canoa and Jama formations), which represent the most diverse Neogene paleodiversity known from the Eastern Pacific coast of Tropical America. In the case of the assemblages from Venezuela, which include the description of the new carcharhinid †*Carcharhinus caquetius* sp. nov. (Figure 1B), the habitat preference of the living counterparts of the fauna recovered from the Urumaco sequence (Socorro, Urumaco and Codore formations), suggest marine shallow waters and estuarine habitats associated with a geographic area connected with a hydrographic system that flowed from western Amazonia up to the Proto-Caribbean Sea during the Miocene (e.g. Sánchez-Villagra et al., 2010; Aguilera et al., 2013). These assemblages from the Urumaco sequence could be useful to understand the ecological role that elasmobranchs played in these ancient transitional environments (Aguilera and Rodrigues de Aguilera, 2004; Aguilera 2010). In addition, the assemblage from the Cantaure Formation, which is hypothetically associated to a shallow-insular high productive marine environment, represents the most diverse elasmobranch fauna known to the early Miocene of the America continent. Its paleodiversity characterized by 39 shark and ray species, with a predominance of benthopelagic sharks with piscivorous

durophagous/cancritrophic feeding preferences, represent a unique glimpse into elasmobranch dietary composition and food chain in the ancient proto-Caribbean Sea.

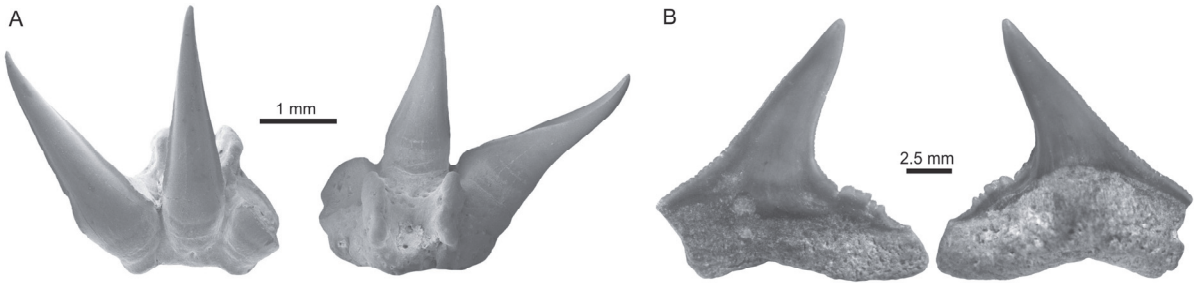


Figure 1. Specimens of new species of deep (A) and shallow (B) waters described in this work. A. †*Chlamydoselachus landinii* sp. nov. (PPP-3455-T-1), from the late Miocene of Ecuador, and B. †*Carcharhinus caquetius* sp. nov. (AMU-CURS-499), from the late Miocene of Venezuela.

The known Tropical America extant chondrichthyan diversity is characterized by a total of 276 species of chimaeras, sharks and rays (Eastern Pacific: 145 spp.; Western Atlantic 181 spp.; see Chapter 1). Notwithstanding the fragmentary nature of the fossil record, it can offer new insights to understand the origin and distribution pattern of the living species from this marine tropical area. One approximation to the chondrichthyan palaeodiversity from Tropical America is presented in the Figure 2, where a comprehensive Miocene-Pleistocene total faunal compilation based on new and published data is presented. The data were standardized at the generic level; in order to remove biases caused by taxonomic and nomenclatural uncertainties at the species level.

Throughout the Neogene the paleodiversity of Tropical America has not been the same, especially shark genera, in both Eastern Pacific and Western Atlantic (Figure 2). The differences could be the result to a significant extent of biases resulting from the scarce chondrichthyan fossil record known of the region, especially in the Eastern Pacific. The clear

difference between sharks and rays paleodiversity could be affected by biases introduced by sampling of dental elements, especially those associated with size. Usually, shark and ray (e.g. Myliobatidae and Rhinopteridae) teeth, due their bigger size, have more probabilities to be surface-collected directly from the outcrop. In contrast, dental elements of many ray and shark species [e.g. many species of Squaliformes and Carcharhiniformes (Scyliorhinidae)], are characterized by micro-teeth, requiring special collecting technics such as screen-washing and microscopically picking. With the exceptions of the assemblages described herein (chapters 2-6), and those previously referred by Laurito (1999), Aguilera and Rodrigues de Aguilera (2001) and Pimiento et al. (2013a, b), little was known about the Tropical America shark/ray paleodiversity based on micro-dental elements. In addition, an important contrast in the number of genera affecting both shark and ray paleodiversity, can also be observed in the Pleistocene fossil record (Figure 2). At first glance it appears that this low Pleistocene diversity could be related to an extinction process. However, the answer for this low paleodiversity is sampling bias. Pleistocene units from Tropical America with chondrichthyan assemblages are extremely rare, including only few taxa from Eastern Pacific (Ecuador and Panama) and Western Atlantic (Venezuela) (Aguilera, 2010; Chapter 1; Carrillo-Briceño and Sánchez-Villagra in prep.).

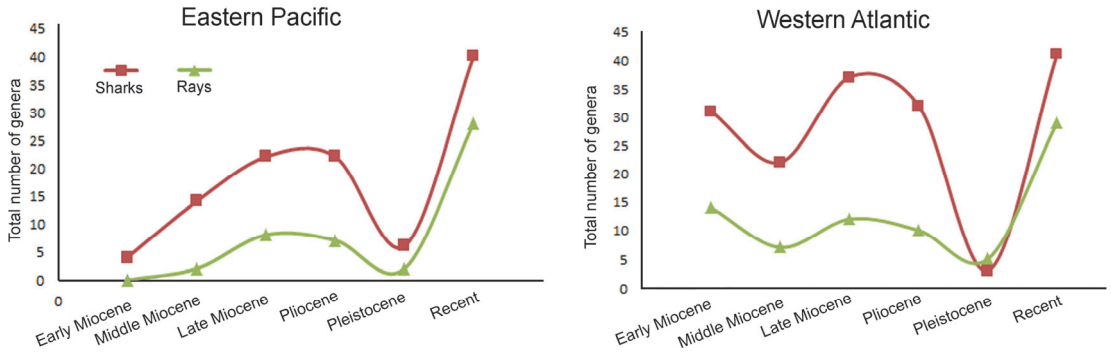


Figure 2. Neogene chondrichthyan paleodiversity of Tropical America in both Eastern Pacific and Western Atlantic. From Carrillo-Briceño and Sánchez-Villagra (in prep).

Tropical marine areas in both Eastern Pacific and Western Atlantic are environmentally heterogeneous (Spalding et al., 2007), with a marked differentiation referable to abiotic variables such as temperature, salinity, bathymetry, coastal length, currents, continental platform, rivers discharge to the oceans, among others (e.g. Miloslavich et al., 2011). These variables changed especially after the rise of the Central American land bridge (e.g. O'Dea et al., 2007a; Coates, and Stallard, 2013), and affected the marine biota (e.g. O'Dea et al., 2007a). The differential pattern in extant chondrichthyan diversity from Tropical America in both Eastern Pacific and Western Atlantic shown in Figure 4 (Chapter 1) could be a direct consequence of changes in the above mentioned variables, as well as other biotic/ecological variables (e.g. food resources, physiological conditions). Assuming the above, the question arises: Did the biotic/abiotic variables in both Eastern Pacific and Western Atlantic explain the chondrichthyan paleodiversity patterns shown in Figures 2-3, or are these mainly the result of sampling bias? The pattern surely reflects real phenomena. However, with the currently paleodiversity known (Figure 2), accurate interpretations are still preliminary. These strategies would be followed to improve this situation. 1) Increase the number of studied assemblages with accurate environmental (e.g. paleobathymetric analysis) and paleoecological inferences (e.g., dietary composition and feeding and habitat preferences). 2) Use of geochemical analysis (e.g. stable isotope on dental elements) of the known chondrichthyan assemblages, used to infer paleotemperatures and paleosalinity levels. Our ongoing work of the assemblages from the early Miocene of Brazil (Pirabas Formation) and Colombia (Jimol and Castilletes formation) (Carrillo-Briceño et al., and Aguilera et al., both in prep.), includes the use of stable isotope in sharks and rays teeth.

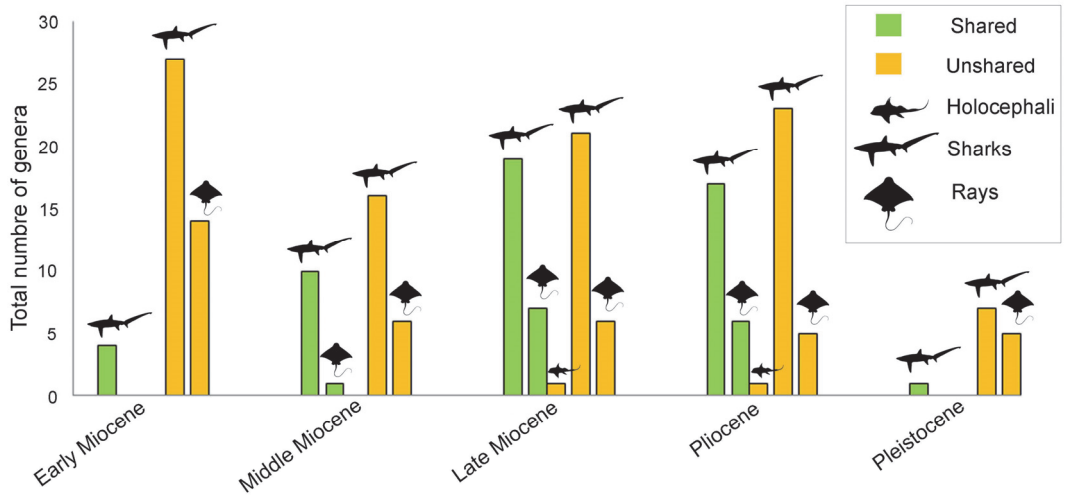


Figure 3. Shared/Unshared fossil genera in both the Eastern Pacific and Western Atlantic. From Carrillo-Briceño and Sánchez-Villagra (in prep).

Taking under consideration a plausible chondrichthyan faunal interchange through marine corridors in the Panamanian area before the definite closure of the isthmus (e.g. Montes et al., 2012, 2015; Coates and Stallard, 2013) we should expect a high taxonomic commonality between Eastern Pacific and Western Atlantic chondrichthyans, with a faunal turnover suggesting environmental changes towards the end of the Neogene. In contrast, Figure 3 shows a pattern where unshared genera (especially sharks) are dominant in all Miocene-Pliocene assemblages. The strong difference observed in early Miocene assemblages, could be assumed due the scarce Eastern Pacific assemblages known from this time (see chapter 6). The numbers of shared/unshared genera are more similar in middle Miocene-Pliocene assemblages; besides the fossil biases, the high proportion of unshared shark genera could be a response to differences in the proportion of the studied paleoenviroments. Most of the fossil assemblages known from Tropical America are

associated to shallow waters, while those associated to deep environments have been scarcely studied (chapters 2-3, 5). One example are Squalomorphii sharks (especially Hexanchiformes and Squaliformes taxa), associated to deep water environments, better known in the fossil record from the Western Atlantic assemblages (chapters 3, 5; Carrillo-Briceño and Sánchez-Villagra, in prep).

Our survey (Figures 2-3), still does not offer a direct biostratigraphic inference to support any of the two postulated timings proposed for the closure of the Panama Isthmus (e.g. Montes et al., 2012, 2015; Coates and Stallard, 2013). However, clues related with possible consequence of "post-Isthmus" environmental changes can be observed. Our analysis (Carrillo-Briceño and Sánchez-Villagra, in prep) reveal regional or complete extirpation of many Eastern Pacific and Western Atlantic shark/ray taxa (mainly neritic/epipelagic species) from Tropical America (Table 1), especially during late Miocene-Pliocene times. At least three genera became regionally extirpated in the Eastern Pacific (*Centrophorus*, *Pristiophorus* and *Carcharhias*) and two in the western Atlantic (*Heterodontus* and *Aetomylaeus*). Moreover, another 13 genera became extinct in both Eastern Pacific and Western Atlantic oceans (*Trigonognathus*, *Nebrius*, *Chiloscyllium*, †*Cosmopolitodus*, †*Carcharocles*, †*Anotodus*, *Hemipristis*, *Paragaleus*, †*Paratodus*, †*Pachyscyllium*, †*Kruckowlamna*, *Rhynchobatus*, and †*Plinthicus*). This late Neogene chondrichthyan extirpation/extinction in both Eastern Pacific and Western Atlantic relatively coincides with the extinction rate of other marine groups (corals and mollusks) in the Caribbean area (O'Dea et al., 2007a, fig. 3).

Taxon				Status		Habitat preferences	
				Eastern Pacific	Western Atlantic	Neritic/ Epipelagic	Bathyal/Meso-Bathypelagic
Squalomorphii	Squaliformes	Squalidae	*Centrophorus*	RE	P		X
		Etmopteridae	*Trigonognathus*	RE	RE		X
	Pristiophoriformes	Pristiophoridae	*Pristiophorus*	RE	P	X	X
Galeomorphii	Heterodontiformes	Heterodontidae	*Heterodontus*	P	RE	X	
	Orectolobiformes	Hemiscyllidae	*Chiloscyllium*	RE	RE	X	
		Ginglymostomatidae	*Nebrius*	RE	RE	X	
	Lamniformes	Odontaspidae	*Carcharias*	RE	P	X	
		Lamnidae	†*Cosmopolitodus*	W-Ext		X	?
		†Otodontidae	†*Carcharocles*	W-Ext		X	?
			†*Paratodus*	W-Ext		X	?
		Alopiidae	†*Anotodus*	W-Ext		X	?
	Carcharhiniformes	Scyliorhinidae	†*Pachyscyllium*	W-Ext		X	?
		Hemigaleidae	*Hemipristis*	RE	RE	X	
			Paragaleus	RE	RE	X	
		Carcharhinidae	†*Kruckowlamna*	W-Ext		X	?
Batiomorphii	Rajiformes	Rhynchobatidae	*Rhynchobatus*	RE	RE	X	
		Myliobatidae	*Aetomylaeus*	P	RE	X	
		Mobulidae	†*Plinthicus*	W-Ext		X	?

Table 1. Extirpated/extinct chondrichthyan taxa from Tropical America. Status: Regional extirpated (RE), extant species presented on the region (P), species worldwide extint (W-Ext). †: extinct taxon.

The future study of the chondrichthyan paleodiversity of Tropical America could be focused on these objectives:

- Continuation of the studies of fossil assemblages in both Eastern Pacific and Western Atlantic, especially in search of micro-dental elements, which could offer new information about poorly studied fossil groups, such as Rajiformes and Torpediniformes, among others, especially those with dental remains below a size of 2 mm (not sampled in the current work).

- Increased use of stable isotope analysis in fossil assemblages [e.g. the ongoing oxygen isotope composition analysis for assemblages from the early Miocene of Colombia and Brazil (Carrillo-Briceño et al., and Aguilera et al., both in prep.)], which are used as proxies for describing environmental and ecological conditions.

- Increased efforts in Pleistocene geological units, due the scarce diversity known from that period. It was in that time, after the definitive closure of the Isthmus of Panama, when different oceanographic events occurred in the region, triggering the beginning of the currently chondrichthyan diversity in both Eastern Pacific and Wester Atlantic oceans. Added to this, the incursion of new methods, such as molecular analysis of chondrichthyan genera present in both side of the Isthmus of Panama, using time-calibrated hypothesis, could be useful to infer divergences and speciation patterns.

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APPENDIX I

Late Neogene elasmobranch fauna from the Coquimbo Formation, Chile

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LATE NEOGENE ELASMOBRANCH FAUNA FROM THE COQUIMBO FORMATION, CHILE

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ABSTRACT – Neogene marine sediments from Chilean geological formations contain a diverse marine fossil fauna. In Chile, the "Norte Chico" (27°S to 32°S) is composed of two important sedimentary marine deposits, the Bahía Inglesa and Coquimbo formations. Diverse vertebrate taxa including fish, birds, mammals and abundant chondrichthyans have been described from Bahía Inglesa Formation. However, the vertebrate fauna from Coquimbo Formation has been poorly documented. Based upon field trips and the analysis of collections from the Coquimbo Formation, the elasmobranch fossil fauna is composed of at least nine taxa, two of which are extinct (*Carcharocles megalodon* and *Carcharodon plicatilis*). The rest of the taxa are related with living elasmobranch species that are inhabitants of the Eastern Pacific Ocean and Tropical America coast.

Key words: Neogene, shark, elasmobranch, chondrichthyans, Coquimbo Formation, Pacific.

RESUMO – Sedimentos marinhos de formações geológicas chilenas do Neógeno contêm uma diversa fauna fóssil marinha. No Chile, o "Norte Chico" (27°S to 32°S) é composto de dois importantes depósitos sedimentológicos marinhos, as formações Bahía Inglesa e Coquimbo. Uma diversidade de táxons de vertebrados, que inclui peixes, aves, mamíferos além de abundantes chondrichthies, têm sido descritos para a Formação Bahia Bahía Inglesa. Entretanto, a fauna de vertebrados da Formação Coquimbo está pobremente documentada. Com base em trabalhos de campo, bem como na análise de coleções da Formação Coquimbo, observa-se uma fauna de elasmobrâquios composta de pelo menos nove táxons, dois dos quais estão extintos (*Carcharocles megalodon* e *Carcharodon plicatilis*). Os demais táxons estão relacionados com as espécies de elasmobrânquios recentes que habitam as costas leste do Oceano Pacífico Leste e da América Tropical.

Key words: Neógeno, tubarão, elasmobrânquio, condrictios, Formação Coquimbo, Pacífico.

INTRODUCTION

Evidence of fossil elasmobranchs has been collected from Neogene marine sediments distributed all over the world (Cappetta, 2012). As an example, fossil elasmobranch teeth have been collected and studied from four main Chilean geological formations: Bahía Inglesa (27°S), Coquimbo (between 29°S to 30°S), Horcón (32°S) and Navidad (33°S) (Philippi, 1887; Gigoux, 1944; Long, 1993; Arratia & Cione, 1996; Suárez & Encinas, 2002; Suárez & Marquardt, 2003; Suárez *et al*., 2004; Carrillo-Briceño *et al*., 2013). These marine fossil deposits have been commonly found in the northern coast of Chile, and characterized by a high proportion of fossil elasmobranch teeth (*e.g*. Suárez & Marquardt, 2003). This particular geographic area is called the "Norte Chico", and is composed of two geological formations: Bahía Inglesa and Coquimbo. The Bahía Inglesa Formation was deposited under marine conditions, and has been well studied geologically (Rojo, 1985; Marquardt, 1999). Different taxa of fish, birds and mammals have been referred from Bahía Inglesa (Long, 1993; Arratia & Cione, 1996; Walsh & Hume, 2001; Walsh & Naish, 2002; Suárez *et al*., 2004; Acosta *et al*., 2006; Chávez, 2008), and at least 23 taxa of chondrichthyan species have been described as well (Long, 1993; Arratia & Cione, 1996; Suárez & Marquardt, 2003; Suárez *et al*., 2004). Unfortunately, craftsmen and private collectors recurrently visit the marine sediments in Bahía Inglesa to remove and sometimes sell the fossils.

In comparison with the knowledge of the marine vertebrate fauna from Bahía Inglesa, little is known about the vertebrate marine fossil fauna from the Coquimbo Formation (Philippi, 1887; Long, 1993). The area of Coquimbo has experienced urban and industrial expansion during the last two decades. Consequently, most of the marine fossil deposits have been disturbed, and many of them are now destroyed or buried. In this context, the aim of this study was to characterize the elasmobranch fossil marine deposits from the Coquimbo Formation by describing fossil teeth found under the surface ground layer before the complete destruction of the locality.

Figure 1. A, map showing the regional representation of Chile. The Coquimbo region is shown in gray color. **B**, zoom in of the Coquimbo region; the gray square represents the study area. The light gray lines are indicating the fourteen areas distributed in this region. **C**, map showing the locations where the elasmobranch fossils were found. The black dot represents the locations: **1**, Caleta Chañaral; **2**, Punta de Choros; **3**, Caleta Hornos; **4**, La Cantera Baja; **5**, Quebrada El Culebrón; **6**, Quebrada Las Rosas; **7**, La Herradura; **8**, El Rincón.

MATERIAL AND METHODS

The material examined consists of isolated elasmobranch fossil teeth that have been collected in different locations from the Coquimbo Formation: Caleta Chañaral, Punta de Choros, Caleta Hornos, La Cantera Baja, La Herradura, Quebrada Las Rosas and El Rincon (Figure 1). The localities La Cantera Baja, La Herradura and Quebrada Las Rosas were already impacted by urbanization. The sampling design consisted of alternating between surface surveys and bulk samples with excavations of up to 1 m depth. Fossil shark teeth are commonly found in the surface layer in the Coquimbo Formation.

This material is deposited at the Museo Arqueológico de La Serena (**MALS**), La Serena, Chile. The classifications follow Compagno (1973, 1977) and the terminology is based on Cappetta (2012). Measurements taken include height and width, and these refer to the entire tooth including the root. Taxonomic identification included an extensive bibliographical review and comparative studies of fossil and extant specimens from: Museo Nacional de Historia Natural de Santiago (**SGO-PV**) in Chile, Museo Paleontológico de Caldera (**MPC**), Atacama, both in Chile and Natural History Museum of Basel (**NMB**), Switzerland; Paleontological collections of the Alcaldía Bolivariana de Urumaco (**AMU-CURS**), Venezuela; Palaeontological Institute and Museum at the University of Zurich (**PIMUZ**), Switzerland.

GEOLOGICAL SETTINGS

Flat terraces of sedimentation characterize the Coquimbo Formation. These are composed of neritic or sublittoral marine sediments that are fine to medium-grained (Le Roux *et al*., 2004). Small-cemented yellowish sand is also present, along

with blocks displaced from the bedrock. Shell middens are commonly found in banks between 0.40 and 2 m thickness, on the surface or in sectors with a whitish calcareous crust on the ground (Paskoff, 1970; Le Roux *et al.*, 2004; Acosta *et al.*, 2006). Although the shell middens are mostly from the Plio-Pleistocene, the Miocene transgression seems to be mostly responsible for most of the marine sediment (Le Roux *et al.*, 2006). In this study, shark fossil teeth were obtained from areas near beaches such as marine terraces close to the sea or streams. The terraces have a relative distance of up to 2 km from the coastline and a peak height of 81 meters (Le Roux *et al.*, 2006). Paskoff (1970) suggests a height of 80 m for the outcrop of the Miocene transgression, but some shark fossil teeth can be found in secondary deposits due to relief changes associated with neotectonics. These changes were very important in structuring the relief of the coast during the Plio-Quaternary (Radtke, 1989).

The age of the Coquimbo Formation could be extended backward in time to about 15 Ma (middle Miocene). Fossil invertebrates suggest that all locations sampled in this study originated from Pliocene sedimentary depositions of marine fauna (Herm, 1969). A study based on the potassium-argon radioisotope suggests that the Coquimbo Formation is upper Miocene in age, of around 6 million years ago (Chávez *et al.*, 2007). In addition, thirteen stratigraphic units were identified in the Coquimbo Formation using faunal remains and lithological features (Le Roux *et al.*, 2004). A maximum age of 2 Ma was estimated using strontium from microfossil remains found in the top of the stratigraphic unit (middle Miocene to late Pliocene; Le Roux *et al.*, 2004). The second stratigraphic unit is from Langhian sediment and it has associated with the base of the Coquimbo Formation (Le Roux *et al.*, 2004; Acosta *et al.*, 2006). As a result of these estimations, we propose an age close to the middle Miocene-late Pliocene for the Coquimbo Formation.

The stratigraphic sequence from Quebrada Las Rosas is composed of marine invertebrates and vertebrates (see Figure 2). The basal stratum comprised lime and clay with fossil mollusks and shark teeth. The median stratum is sandy and made of conglomerates of mollusks. The upper stratum is formed of fine sand with a layer of invertebrates. However, this is a general description and we are not able to provide further details because of the lack of stratigraphic studies. A similar formation is observed in Bahía Inglesa Formation (**BIF**) with common records of shark teeth composed of a large spectrum of taxa (Suárez & Marquardt, 2003; Rivadeneira & Varas, 2012).

SYSTEMATIC PALEONTOLOGY

Order LAMNIFORMES Berg 1937
Family †OTODONTIDAE Glikman, 1964

†*Carcharocles* Jordan & Hannibal, 1923

†*Carcharocles megalodon* (Agassiz, 1843)
(Figures 3A-C)

Material. Four lower lateral teeth (MNHN SGO. 58, Coquimbo; MALS P-228, Punta de Choros; MALS P-6564, Quebrada Chañaral de Aceitunas; MALS P-227, Quebrada El Culebrón).

Description. Teeth have a triangular, broad and slightly symmetrical crown. The lingual face of the crown is flat and the labial is convex with a typical large neck, clearly observed in the specimen MNHN SGO. 58. The crown in the rest of the specimens is poorly preserved. Both cutting edges have a fine serration. The root has well developed lobes and a weak lingual protuberance. The teeth range in height between 32 and 98 mm and width between 35 to 93 mm. The largest tooth is the specimen MALS P-228, with 98 mm in height and 93 mm in width.

Remarks. *Carcharocles* was a cosmopolitan species and its fossil record has been reported from almost all Neogene sedimentary deposits that contain shark teeth (García *et al.*, 2009). In the Neogene deposits, *Carcharocles* is mainly represented by *C. chubutensis* Ameghino, 1901 and *C. megalodon* Agassiz, 1843 (*e.g.* Pimiento *et al.*, 2010, 2013a,b; Cappetta, 2012; Pimiento & Clements, 2014). *C. megalodon* has a stratigraphic range from the middle Miocene to the late Pliocene (Pimiento & Clements, 2014), whereas *C. chubutensis* has been restricted to the early/middle Miocene (Pimiento & Clements, 2014). However, taxonomical distinctions and generic identification between the taxa have been debated over the years. The classification of *Carcharocles* linage is still discussed (Pimiento *et al.*, 2010, 2013b; Reinecke *et al.*, 2011; Cappetta, 2012; Bor *et al.*, 2012). From the Neogene of Chile, *C. megalodon* has been reported from the Bahía Inglesa and Lo Abarca formations (Long, 1993; Walsh, 2001; Encinas, 2002; Suárez & Encinas, 2002; Suárez *et al.*, 2004). Philippi (1887) reported an isolated tooth of *C. megalodon* with unclear origin from Coquimbo region. The specimens of *C. megalodon* from the Coquimbo Formation extend the southern distribution on the Eastern Pacific during the late Neogene. An overview of the *C. megalodon* is show by Carrillo-Briceño *et al.* (2013) from America fossil records.

Family LAMNIDAE Müller & Henle, 1838

Carcharodon Smith *in* Müller & Henle, 1838

Carcharodon carcharias Linnaeus, 1758
(Figure 4A)

Material. Fifty upper lateral teeth (MALS P-59, MALS P-60, MALS P-64, Quebrada El Culebrón; MALS P-79, MALS P-80, MALS P-83, MALS P-84, MALS P-86, MALS P-87, MALS P-88, MALS P-90, MALS P-92, MALS P-105, La Cantera Baja; MALS P-119, MALS P-126, MALS P-127, Quebrada Las Rosas; MALS P-131, MALS P-133, Caleta Chañaral; MALS P-142, MALS P-143, MALS P-144, MALS P-150, MALS P-151, MALS P-152, MALS P-159, MALS P-160, MALS P-161, MALS P-163, MALS P-164, MALS P-165, MALS P-166, MALS P-169, MALS P-170,

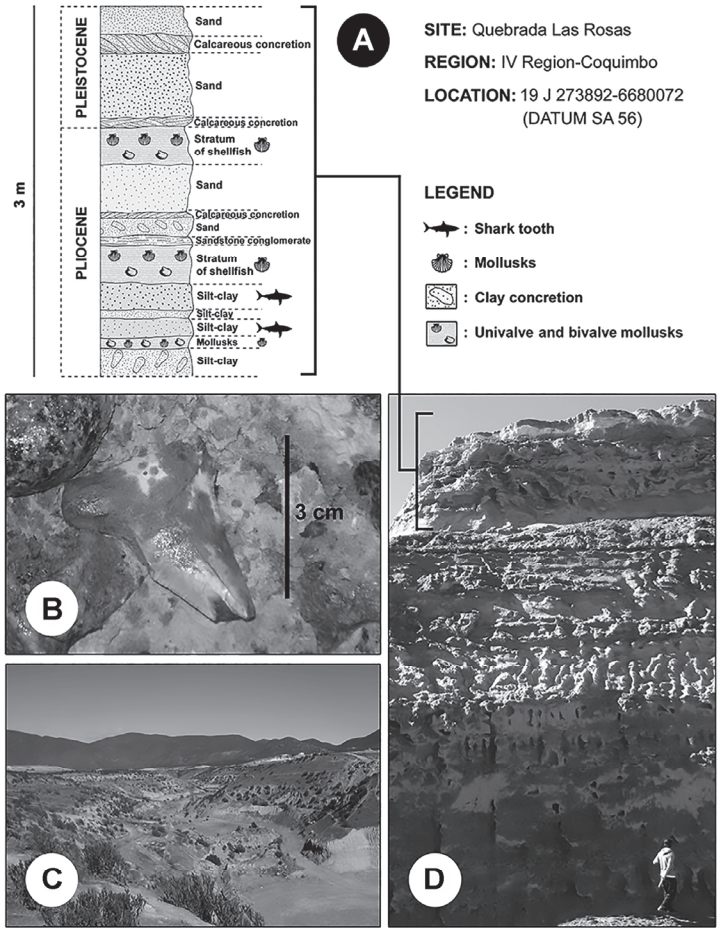

Figure 2. A, geological stratigraphic units showing the association of elasmobranchs found in the Coquimbo Formation. **B**, *Carcharodon carcharias* fossil tooth found on silt-clay mixed with stones and sedimentary soil. **C**, landscape of sedimentary terraces of the Coquimbo Formation located in Quebrada Las Rosas. **D,** general view of stratigraphic units from Quebrada Las Rosas.

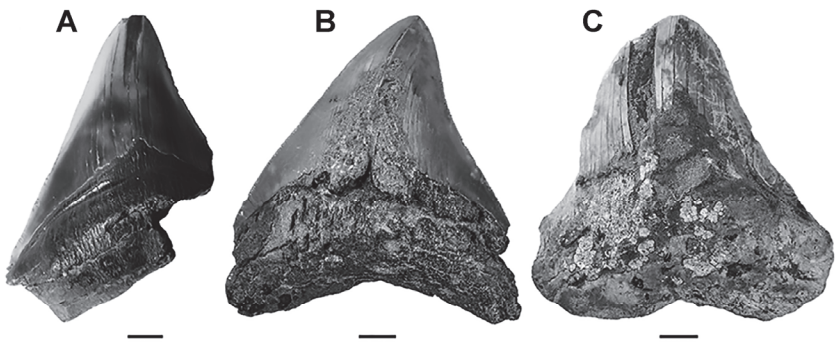

Figure 3. *Carcharocles megalodon* fossil teeth. **A**, MNHN SGO.58, lower lateral tooth in labial view; **B**, MALS P-6564, lower lateral tooth in labial view; **C**, MALS P-228, lower lateral in labial view. Scale bars = 10 mm.

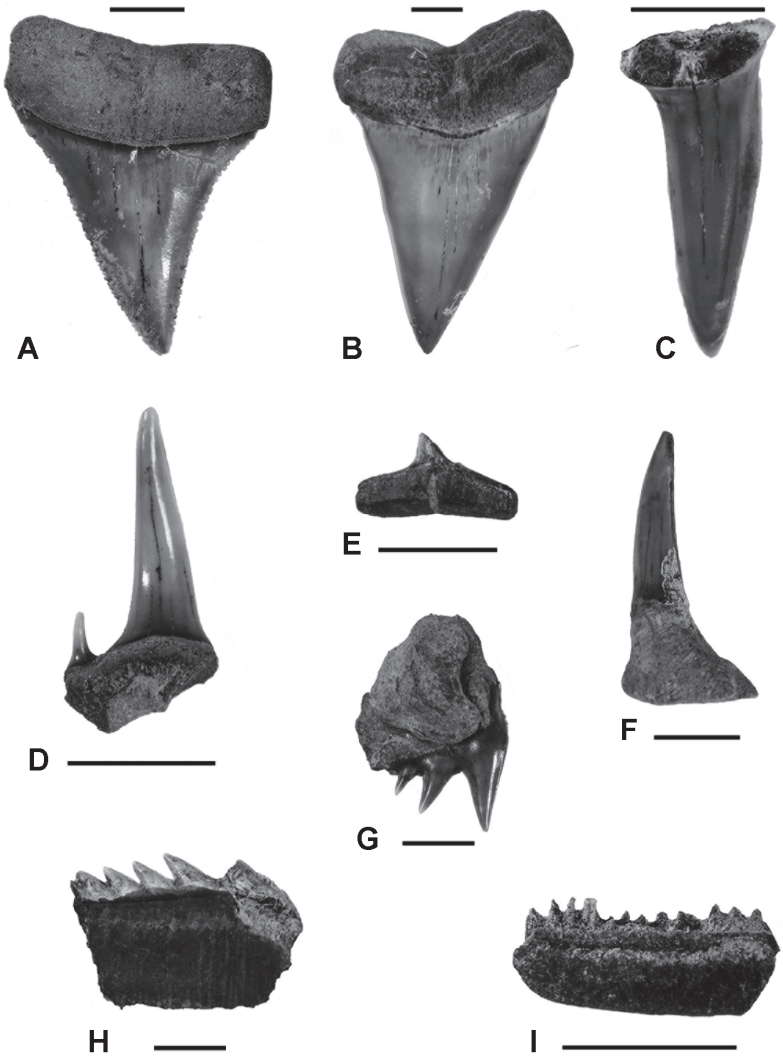

Figure 4. Elasmobranch fossil teeth. **A**, *Carcharodon carcharias*, MALS P-87, upper lateral tooth in labial view. **B**, *Carcharodon plicatilis*, MALS P-63, upper lateral tooth in labial view. **C**, *Isurus* cf. *I. oxyrinchus*, MALS P-199, upper anterior tooth in labial view. **D**, *Odontaspis ferox*, MALS P-104, lateral tooth in labial view. **E**, *Carcharhinus* sp. MALS P-111, lower lateral tooth in labial view. **F**, *Pristiophorus* sp., MALS P-75, rostral tooth. **G**, *Hexanchus* cf. *H. griseus*, MALS P-108, upper anterior tooth in lingual view. **H**, *Hexanchus* cf. *H. griseus*, MALS P-225, lower lateral tooth in lingual view. **I**, *Myliobatis* sp., MALS P-231, symphysial tooth of in lingual view. Scale bars = 10 mm.

MALS P-176, MALS P-177, MALS P-178, MALS P-179, MALS P-184, MALS P-189, MALS P-190, MALS P-193, MALS P-197, MALS P-198, La Herradura; MALS P-203, MALS P-206, MALS P-208; MALS P-212, MALS P-216, MALS P-217, MALS P-219, Quebrada El Culebrón), one upper posterior tooth (MALS P-114, La Cantera Baja), three upper teeth (MALS P-147, MALS P-181, MALS P-185, La Herradura), ten upper anterior teeth (MALS P-85, MALS P-93, La Cantera Baja; MALS P-116, Quebrada Las Rosas; MALS P-146, MALS P-155, MALS P-186, MALS P-191, MALS P-194, La Herradura; MALS P-210, MALS P-220, Quebrada El Culebrón), three lower posterior teeth (MALS P-78, MALS P-113, La Cantera Baja; MALS P-148, La Herradura), fourteen lower lateral teeth (MALS P-81, MALS P-82, MALS P-91, La Cantera Baja; MALS P-129, MALS P-130, Quebrada Las Rosas; MALS P-145, MALS P-149, MALS P-171, MALS P-196, La Herradura; MALS P-207, MALS P-209, MALS P-211, MALS P-2014, MALS P-215, Quebrada El Culebrón), six lateral teeth (MALS P-117, MALS P-128, Quebrada Las Rosas; MALS P-153, MALS

P-162, MALS P-173, La Herradura; MALS P-223, Quebrada El Culebrón), twenty lower anterior teeth (MALS P-89, La Cantera Baja; MALS P-141, MALS P-154, MALS P-156, MALS P-168, MALS P-172, MALS P-174, MALS P-180, MALS P-182, MALS P-183, MALS P-192, MALS P-195, La Herradura; MALS P-204, MALS P-205, MALS P-213, MALS P-218, MALS P-221, MALS P-222, MALS P-224, Quebrada El Culebrón) and one unknown position tooth (MALS P-157, La Herradura).

Description. Upper and lower teeth have a broad, triangular and slightly elongated labio-lingually compressed crown. The labial face is flattened whereas the lingual is convex; both cutting edges are coarse serrated. The basal portion of the crown is in contact with roots and lacks enamel, forming a thin dental band, observable on the labial and lingual surface. Root with two well-defined lobes that are straight or it may present a U-shaped arch in some specimens. The teeth range in height between 10 and 73 mm and width between 10 to 47 mm.

Remarks. The fossil record of *Carcharodon carcharias* is known from the lower Pliocene to recent, and it has been referred to Africa, Asia, Australia, Europa and North and South America (Kemp, 1991; Cappetta, 2012; Ehret *et al.*, 2012, Cione *et al.*, 2012; Carrillo-Briceño *et al.*, 2013). The fossil record of *C. carcharias* from the late Neogene of Chile is abundant, mainly from the Pliocene strata of the Bahía Inglesa Formation (Long, 1993; Walsh, 2001; Quilodran & Marquardt, 2001; Walsh & Naish, 2002; Suárez & Marquardt, 2003). However, some specimens have been dubiously referred to the late Miocene strata of this unit (*e.g.* Bianucci *et al.*, 2006). Other fossil record of *C. carcharias* from Chile include the following localities: Bahía Salado, Bahía Tongoy, Cuenca del Tiburon, Horcón, La Cueva, and La Portada (Suárez & Brito, 2000; Emslie & Correa, 2003; Suárez & Marquardt, 2003; Le Roux *et al.*, 2006; Carrillo-Briceño *et al.*, 2013). Cione *et al.* (2012) and Carrillo-Briceño *et al.* (2013) provided a summary of the fossil record of *C. carcharias* in South America.

†*Carcharodon plicatilis* Agassiz, 1843
(Figure 4B)

Material. Upper lateral tooth (MALS P-63, El Rincón).

Description. The tooth has a wide, triangular and labio-lingually compressed crown. The cutting edges are sharp without any serration. The root is compressed with two lobes, and the base shows a concavity forming an inverted V. The tooth measures 50 mm in height and 36 mm in width.

Remarks. Several morphological aspects of the taxonomic classification of this species have been debated over the years, without consensus (*e.g.* Purdy *et al.*, 2001; Cappetta, 2012; Cione *et al.*, 2012; Ehret *et al.*, 2012). Previous taxonomic assignments have included some species of "wide-toothed shape" such as *Isurus planus* Agassiz, 1856, *Isurus hastalis* Agassiz, 1838 and *Isurus xiphodon* Agassiz, 1838 to *Cosmopolitodus* (Cappetta, 2006, Cione *et al.*, 2012). Ehret *et al.* (2012) included *Cosmopolitodus* to *Carcharodon*, proposing a transition between *Carcharodon hastalis* and *Carcharodon carcharias*. Ward & Bonavia (2001) suggested the recognition of only one species, and proposed that *C. xiphodon* is a *nomen dubium* because of the uncertainty implied in differentiating *Cosmopolitodus hastalis* from *Cosmopolitodus xiphodon*. According to Cione (1988), Purdy *et al.* (2001) and Cione *et al.* (2012), there is a species that appears to be the putative sister group of *Carcharodon carcharias* and different from *Cosmopolitodus hastalis*. Cione *et al.* (2012) proposed this species as "*Isurus*" *plicatilis* Agassiz, 1843, which is recognized as an available and valid taxon. According to Cione *et al.* (2012), only *plicatilis* or *xiphodon* [adapting latter from Purdy *et al.* (2001)] should be referred to the genus *Carcharodon*. Hereby, we adopt the taxonomic proposal suggested by Cione (1988) and Cione *et al.* (2012). In the Neogene of Chile, *Carcharodon plicatilis* has been reported from the Bahía Inglesa, Navidad and Coquimbo formations (Long, 1993; Quilodran & Marquardt, 2001; Walsh, 2001; Suárez & Encinas, 2002; Walsh & Naish, 2002; Suárez & Marquardt, 2003; Le Roux *et al.*, 2006).

Isurus Rafinesque, 1810

Isurus cf. *oxyrinchus* Rafinesque, 1810
(Figure 4C)

Material. Upper lateral tooth (MALS P-58, Caleta Chañaral), upper anterior tooth (MALS P-199, Caleta de Hornos), lower anterior tooth (MALS P-134, Caleta Chañaral) and anterior tooth, unknown jaw position (MALS P-188, La Herradura).

Description. Three teeth are incomplete with damaged roots (MALS P-134, MALS P-188, MALS P-199). In anterior teeth the crown is elongated, asymmetrical, distally inclined and with smooth sharp cutting edges; its apex is sharp-pointed. The lateral has a triangular crown slightly inclined distally. There is an evident lingual protuberance with a transverse groove. The only complete tooth (MALS P-58) measures 25 mm in height and 12 mm in width.

Remarks. *Isurus oxyrinchus* has a stratigraphic record from the late Oligocene to present with a cosmopolitan paleodistribution (Reinecke, 2011). Despite the fact that the specimens from the Coquimbo Formation are mostly incomplete, they exhibit a close resemblance to teeth of the extant *I. oxyrinchus*, allowing the association of the fossils with this taxon. In Chile, the fossil record of *I. oxyrinchus* appears regularly along the central coast of the Bahía Inglesa Formation (Suárez *et al.*, 2002; Walsh, 2001; Long, 1993; Suárez & Marquardt, 2003; Suárez *et al.*, 2004). In contrast to Bahía Inglesa, *I. oxyrinchus* fossil teeth are less frequent southward. However, this species has been found in marine sediments from Lo Abarca, Navidad and Horcón formations (Encinas, 2002; Suárez & Encinas, 2002; Suárez & Marquardt, 2003; Suárez *et al.*, 2006; Carrillo-Briceño *et al.*, 2013).

Family ODONTASPIDIDAE Müller & Henle, 1839

Odontaspis Agassiz, 1838

Odontaspis ferox Risso, 1810
(Figure 4D)

Material. Lateral tooth (MALS P-104, La Cantera Baja).
Description. The crown is elongated and slender with sharp and smooth cutting edges. Fossil and extant specimens of *Odontaspis ferox* show between three and one lateral cusplets (*e.g.* Purdy *et al.*, 2001). However, the specimen MALS P-104 preserves only one cusplet as a consequence of the damaged root. The root shows an evident lingual protuberance. The incomplete tooth is 22 mm in height.
Remarks. *Odontaspis ferox* has a fossil record from the Miocene to recent (Purdy *et al.*, 2001; Aguilera & Rodríguez de Aguilera, 2001; Marsili, 2007). During the Paleocene-Eocene, this species is considered as the dominant group of Patagonia of Chile and Argentina, as well as of other ancient temperate seas around the world (*e.g.* Eocene of Seymour Island, Antarctica) (Arratia & Cione, 1996). This species has been reported to the Bahía Inglesa (Suárez *et al.*, 2002) and Navidad formations (Suárez& Encinas, 2002; Suárez & Marquardt, 2003).

Order CARCHARHINIFORMES Compagno, 1973
Family CARCHARHINIDAE Jordan & Evermann, 1896

Carcharhinus Blainville, 1816

Carcharhinus sp.
(Figure 4E)

Material. Three lower lateral teeth (MALS P-110, MALS P-112, La Cantera Baja; MALS P-111, La Cantera).
Description. The fossil teeth are fragmented, preserving only the crown or the root. The crown is triangular and decreases in size toward the apex of the tooth. The crown is distally inclined towards the right with fine serration along the cutting edges (MALS P-110). The root has broad lobes with slightly basal concavity and a shallow nutritive groove (MALS P-111). Diagnostic characters of the species are difficult to identify because of the fragmented condition and poor preservation of the specimens.
Remarks. Morphological features of the tooth within the genus *Carcharhinus* closely resembles between species. This confusion makes difficult the taxonomic classification of the carcharhinids fossil teeth, especially when they are incomplete and eroded. At least two species have been identified from Chilean marine sediments *i.e. Carcharhinus albimarginatus* (Rüppell, 1837) (Long, 1993; Suárez & Marquardt, 2003) and *Carcharhinus brachyurus* (Günther, 1870) (Suárez *et al.*, 2002; Suárez *et al.*, 2004; Carrillo-Briceño *et al.*, 2013). However, previous studies in modern species have confirmed the presence of other carcharhinids species in Chilean coast. Pequeño & Saez (2003) have reported the presence of *Carcharhinus galapagensis* (Snodgrass & Heller, 1905) from Salas y Gomez Island and Hernández *et al.* (2008) identified the species *Carcharhinus obscurus* (Lesueur, 1818) from shark fins traded in Chilean market. According to these antecedents, the presence of extinct and modern carcharhinids should be better studied in Chile because there are uncertainly in some of the species used to occur and/or still found in Chilean coast. In the Neogene and Quaternary of Chile, species of genus *Carcharhinus* has been reported from the Miocene and Pliocene in the Bahía Inglesa Formation (Long, 1993; Walsh, 2001; Suárez & Marquardt, 2003; Suárez *et al.*, 2002), Bahía Salado (Suárez & Brito, 2000), Cuenca del tiburón (Emslie & Correa, 2003; Suárez & Marquardt, 2003), La Portada (Suárez & Marquardt, 2003) and Horcón (Carrillo-Briceño *et al.*, 2013).

Order PRISTIOPHORIFORMES Berg, 1958
Family PRISTIOPHORIDAE Bleeker, 1859

Pristiophorus Müller & Henle, 1837

Pristiophorus sp.
(Figure 4F)

Material. Thirteen rostral teeth (MALS P-69, MALS P-70, MALS P-71, MALS P-72, MALS P-73, MALS P-74, MALS P-75, MALS P-76, MALS P-77, La Cantera Baja; MALS P-118, Quebrada Las Rosas; MALS P-138, MALS P-139, MALS P-140, La Herradura).
Description. The rostral teeth are elongated and slender, with a dorso-ventrally compressed crown. The cutting edges are smooth and without serration. The root is robust with a flat base and is wider than the crown. The root also has a conical shape with the widest part being the base. Most of the specimens are complete and measure between 31 and 32 mm in length.
Remarks. *Pristiophorus* is known from the upper Cretaceous to present (Cappetta, 2012). The Neogene fossil record of *Pristiophorus* showed a wide paleobiogeographic distribution in America (Carrillo-Briceño *et al.*, 2015). Nowadays, there is only one species in America *Pristiophorus schroederi* Müller and Henle, 1837, which is distributed in the Bahamas region, Western Central Atlantic (Compagno *et al.*, 2005). The taxonomy of the fossil species of *Pristiophorus* found in the Americas, and especially the rostral teeth have been poorly studied. For this reason we prefer to keep the *Pristiophorus* specimen from the Coquimbo Formation in open nomenclature. The fossil record of *Pristiophorus* in Chile includes Bahía Inglesa (Walsh, 2001; Suárez *et al.*, 2002), Navidad (Suárez & Encinas, 2002; Suárez *et al.*, 2006), Horcón (Carrillo-Briceño *et al.*, 2013) and La Cueva formations (Suárez & Marquardt, 2003).

Order HEXANCHIFORMES Buen, 1926
Family HEXANCHIDAE Gray, 1851

Hexanchus Rafinesque, 1810

Hexanchus cf. *griseus*
(Figures 4G-H)

Material. Five upper teeth (MALS P-107, MALS P-108, La Cantera Baja; MALS P-125, Quebrada Las Rosas; MALS P-61, MALS P-226, Quebrada el Culebrón) and a lower lateral tooth (MALS P-109, La Cantera Baja; MALS P-225, Quebrada el Culebrón).

Description. Upper teeth are elongated acrocones that are distally inclined, with two or five distally directed cusplets. The root is flattened and subquadrangular. The lower tooth is incomplete with a missing acrocone (MALS P-225). However, five small and distally directed cusplets are present. The complete teeth range between 16 and 21 mm in height and between 8 to 18 mm in width.

Remarks. *Hexanchus griseus* is known from the Miocene to the recent (Cione & Reguero, 1994). In Chile, *Hexanchus griseus* and *Hexanchus* sp. have been referred to the Bahía Inglesa and Horcón formations (Long, 1993; Walsh, 2001; Suárez & Marquardt, 2003; Carrillo-Briceño *et al.*, 2013). Suárez & Marquardt (2003) referred isolated teeth of *Hexanchus* associated with cetacean remains from phosphatic layer in Caleta Inglesa and Bahía Chañaral. Arratia & Cione (1996) and Carrillo-Briceño *et al.* (2013) presented a brief summary of the fossil record of *Hexanchus* in South America.

Order MYLIOBATIFORMES Compagno 1973
Family MYLIOBATIDAE Bonaparte 1838

Myliobatis Cuvier, 1816

Myliobatis sp.
(Figure 4I)

Material. Six isolated teeth (MALS P-66, MALS P-230, MALS P-231, MALS P-232, MALS P-233, MALS P-234, La Cantera Baja).

Description. The specimens consist of complete isolated teeth of the median files. These teeth are broader than long, with a slightly curved hexagonal contour. In all teeth the crown is practically flat with a smooth occlusal surface. Labial and lingual faces are slightly ornamented. The root displays vascularization type polyaulacorhize. The teeth are between 30 and 50 mm wide.

Remarks. The fossil record of *Myliobatis* extends worldwide from the Paleocene to present (Cappetta, 2012). The taxonomic identification of the isolated teeth of *Myliobatis* is extremely difficult because of the high dental variation within this group (Welton & Zinsmeister, 1980; Nishida, 1990). For this reason, a specific taxonomic assignation was not possible and we assigned all specimens from the Coquimbo Formation to *Myliobatis* sp. In the Neogene of Chile, the genus *Myliobatis* has been found in the Bahía Inglesa, La Cueva and Navidad formations (Walsh, 2001; Suárez & Marquardt, 2003; Suárez *et al.*, 2004; Suárez *et al.*, 2002). Summary of the fossil record of *Myliobatis* is discussed in Carrillo-Briceño *et al.* (2013).

DISCUSSION

Our results revealed at least nine elasmobranch taxa present during the Neogene at the Coquimbo Formation. These include *Carcharocles megalodon*, *Carcharodon carcharias*, *C. plicatilis*, *Isurus* cf. *I. oxyrinchus*, *Pristiophorus* sp., *Odontaspis ferox*, *Carcharhinus* sp., *Hexanchus* cf. *H. griseus* and *Myliobatis* sp. Of these species, *C. megalodon*, *C. plicatilis*, *C. carcharias* and *I. oxyrinchus* have been previously reported from the Coquimbo Formation (*e.g.* Philippi, 1887; Long, 1993; Suárez & Marquardt, 2003; Le Roux *et al.*, 2006). According to our results, *Odontaspis ferox* and *Pristiophorus* sp. represent the first fossil records for the Coquimbo Formation, although Long (1993) included two further species, *Cetorhinus maximus* and *Aetobatus* sp. for this locality. Our assemblage includes at least two extinct species: *C. megalodon* and *C. plicatilis*. With the exception of *Pristiophorus* sp., the rest of the elasmobranch taxa found in this study are related to the living species distributed along the Pacific coast of South America (*e.g.* Egaña & McCosker, 1984; Acuña *et al.*, 2002; Hernández & Lamilla, 2004; Hernández *et al.*, 2008).

The Neogene is characterized as a period of intense climatic, tectonic and biotic change (Zachos, 2001; Dekens *et al.*, 2007; Dowsett & Robinson, 2009; Garreaud *et al.*, 2010). For instance, events such as the hyper-aridity of the Atacama Desert and the reactivation of the modern flow of the Humboldt Current produced important changes in the Neogene climate conditions (Garreaud *et al.*, 2010; Tsuchi, 2002). Studies of elasmobranch fossils suggest vast variations in species richness in the South Pacific (Villafaña & Rivadeneira, 2014). The elasmobranch fossil record of the Coquimbo Formation would suggest differences in the dynamics of elasmobranch biodiversity. Species, such as *Carcharocles megalodon*, *Carcharodon plicatilis* and *Pristiophorus* sp. probably became extinct due to climatic and biotic changes that occurred during the late Neogene. Rivadeneira & Marquet (2007) suggested that the diversity in the composition of mollusk species decreased during the Miocene and Pliocene along the South American Pacific coast. A similar tendency in decreasing diversity was shown with the extinction of marine mammals (Valenzuela-Toro *et al.*, 2013), and sea birds (Chávez *et al.*, 2007). The extinction of several macro-vertebrates may reflect the macro-evolutionary dynamics of those taxa in the temperate Pacific coast of South America.

In addition, we found differences in the distribution of extinct elasmobranch species in comparison to modern species. For example, the fossil distribution of *Carcharodon carcharias* and *Hexanchus* increased southward (Villafaña & Rivadeneira 2013). In contrast, the presence of shark species such as *Isurus oxyrinchus*, *Odontaspis ferox*, *Carcharhinus* sp. and *Myliobatis* sp. decreased southward (Villafaña & Rivadeneira 2013). Analyzing the distribution of genus *Carcharias* in the South Pacific Ocean, it might be attributed to the abrupt temperature decrease during the middle Pliocene and Pleistocene (Cione *et al.*, 2007). This change in the temperature eventually also affected the

distribution other species. However, Villafaña & Rivadeneira (2013) suggested that the fluctuation in elasmobranch biodiversity might also be explained by ecological and life history aspects such as body size, modes of reproduction, and migration patterns.

In order to explain the variability in richness and composition of marine fossil records in Chile, it would be valuable to increase the sampling effort of fossil records from the Coquimbo Formation and other Neogene units. Furthermore, more sampling sites should be determined and reviewed. The well-preserved sedimentary sequence of the Coquimbo Formation is an unexplored field. A better description of the elasmobranch fossil records will set the baseline to gain a better understanding of the ecology, distribution and evolution of taxa that ranged the oceans millions of years ago.

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APPENDIX II

The Path towards Endangered Species: Prehistoric Fisheries in Southeastern Brazil

PLOS | ONE

RESEARCH ARTICLE

The Path towards Endangered Species: Prehistoric Fisheries in Southeastern Brazil

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Data Availability Statement: All relevant data are within the paper and its Supporting Information files. All specimens studied here were deposited in the zooarchaeological collection of Museu Nacional, Universidade Federal do Rio de Janeiro (MNUFRJ-ZA), Parque da Boa Vista, São Cristovão, Rio de Janeiro, Brazil. http://www.museunacional.ufrj.br/ - refers to S1 Appendix. All relevant species specific characters were identified based on comparative anatomy, using otoliths, dry finfish skeletons and shark tooth collections housed at the Universidade Estadual do Rio de Janeiro (UERJ) and Universidade

Abstract

Brazilian shellmounds are archaeological sites with a high concentration of marine faunal remains. There are more than 2000 sites along the coast of Brazil that range in age from 8,720 to 985 cal BP. Here, we studied the ichthyoarchaeological remains (i.e., cranial/post-cranial bones, otoliths, and teeth, among others) at 13 shellmounds on the southern coast of the state of Rio de Janeiro, which are located in coastal landscapes, including a sandy plain with coastal lagoons, rocky islands, islets and rocky bays. We identified patterns of similarity between shellmounds based on fish diversity, the ages of the assemblages, littoral geomorphology and prehistoric fisheries. Our new radiocarbon dating, based on otolith samples, was used for fishery characterization over time. A taxonomical study of the ichthyoarchaeological remains includes a diversity of 97 marine species, representing 37% of all modern species (i.e., 265 spp.) that have been documented along the coast of Rio de Janeiro state. This high fish diversity recovered from the shellmounds is clear evidence of well-developed prehistoric fishery activity that targeted sharks, rays and finfishes in a productive area influenced by coastal marine upwelling. The presence of adult and neonate shark, especially oceanic species, is here interpreted as evidence of prehistoric fisheries capacity for exploitation and possibly overexploitation in nursery areas. Various tools and strategies were used to capture finfish in seasonal fisheries, over rocky reef bottoms and in sandy littoral environments. Massive catches of whitemouth croaker, main target dermersal species of South Atlantic coast, show evidence of a reduction in body size of approximately 28% compared with modern fisheries. Fishery activity involving vulnerable species, especially in nursery areas, could mark the beginning of fish depletion along the southeastern Brazilian coast and the collapse of natural fish populations.

Federal Fluminense (UFF), see more details in the S2 Appendix. Relevant species specific osteological characters were also identified based on extensive bibliographic review.

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Introduction

When investigating early archaeological settlements in Brazil, South America [1], the existence of an undisturbed marine fauna predating European colonization is expected. The archaeological evidence of prehistoric fisheries shows high abundance and diversity of marine faunal remains recovered from Brazilian shellmounds [2,3,4,5,6,7,8,9,10,11,12]. However, the main goal of these studies is to elucidate the archaeological context of fisher-gatherer settlements. The ichthyoarchaeological remains testify to well-developed fisheries for sharks, rays and finfishes, as well as to shellfish gathering and hunting of marine reptiles and mammals. Prehistoric subsistence fisheries could have been the cause of early differential disturbances in local fish fauna resources due to the assumed use of beach seines, gillnets, hook and line, traps and spearfishing.

A key study on prehistoric fisheries in the Caribbean [13] strongly supports the claim that overexploitation did not occur. However, the debate about fish depletion, overexploitation, extinction and environmental degradation in prehistoric and colonial times continues [14,15]. Prehistoric overfishing could be associated with local environmental degradation as a consequence of human uses of the landscape affecting the marine environment, community dynamics and spatially subsidized food webs [16,17,18,19], and overexploitation based exclusively on prehistoric fisheries might not have been the exclusive cause [15,20,21]. This hypothesis was widely discussed using evidence from comparative analyses of Pacific islands and channel ecosystems under archaeological investigation [22,23]. However, tropical Western Atlantic prehistoric fisheries differ in terms of Holocene paleoenvironments, fish assemblages and large-scale vulnerability at the time of prehistoric fisheries along the South American coast ([1]; S1 Appendix).

Prehistoric fishery exploitation patterns along the Atlantic coast of South America, from Brazil to Argentina are not well described. Brazilian shellmounds ranges from 8,720 to 985 years calibrated before present (cal BP) [1,24,25,26,27,28,29,30,31]. Previous ichthyological records from these archaeological sites were documented only by faunal lists without illustrative diagnostic species characters or museum catalog numbers to corroborate the species identifications. The present contribution is an attempt to improve our understanding of Rio de Janeiro's shellmounds by providing new, detailed and accurate taxonomic lists and analyses of the relevant fish assemblages.

Contiguous with south Brazil and Uruguay, Argentinean ichthyoarchaeological sites, situated on the coast of San Matías Gulf in Patagonia (6,800 to 890 yr BP), show evidence of local prehistoric fisheries. The abundance of otoliths indicates that the predominant bony fish target was the whitemouth croaker, *Micropogonias furnieri* [32,33,34,35], a coastal finfish species also present in Brazilian coastal shellmounds.

Fishery tools, such as projectile points, manufactured mainly with bones are frequently recovered from the Brazilian shellmounds [30]. Moreover, evidence that allows us to infer the use of wood and vegetable fiber for the construction of fish traps, beach seines and or gillnets used for massive captures of large fish schools is not preserved. Indirect evidence of boat constructions based on lithic tools and records in detailed rock paintings reveal fluvial skillful navigators in Northeastern of Brazil [36]. In addition, the frequency of skeletal anomalies found in human remains recovered from the shellmounds, including auditory meatus exostoses, osteoarthritis, osteoarthrosis and other degenerative effects [37,38], is usually considered to be a marker of sailing and aquatic labor in cold waters [39,40,41], suggesting the engagement of those human populations in traditional fishery activity for subsistence. Stable isotope analyses of $\delta^{14}C$ and $\delta^{15}N$ in human skeletons from the shellmounds of Southern Brazil indicate a diet strongly dependent on marine resources [42]. Therefore, in agreement with previous research

[43], the abundance and diversity of fish remains from the shellmounds provides unequivocal proof of fisheries that were able to operate in open waters over sandy and rocky bottoms.

Shellmounds are not necessarily horizontally stratified due to sequential periods of occupation, and the areas selected for specific activities may vary from the center to the periphery of the shellmound [44,45]. These sandy shellmounds are usually dome-shaped, and the archaeological variation in vertical section is based on changes in sediment texture and color, settlement size, abundance and diversity of mollusks, intercalation of sterile sandy layers (i.e., without ichthyoarchaeological remains) and evidence of cultural activities (e.g., burials and stoves). However, in contrast with archaeological evidence from settlements, in some shellmounds, the layers could not be distinguished [46].

The Rio de Janeiro shellmounds [1] are located in a coastal landscape characterized by sandy plains with coastal lagoons, rocky islands, islets and rocky bays [47]. These coastal areas are strongly influenced by seasonal upwellings, occurring during the austral summer [48,49,50,51], which increase marine productivity and the potential resources for fisheries.

Therefore, the main goal of this study is to highlight the fish diversity and faunal assemblage of ancient fisheries based on the skeletal remains deposited in the shellmounds along the southeastern Brazilian coast. Additionally, we correlate shark diversity and abundance in the shellmounds with the abilities of specific fisheries to exploit resources, which could lead to overexploitation. The groundfish catches were the result of multi-gear strategies in seasonal fisheries. Radiometric age, geochemical analyses and climate reconstruction of these ichthyoarchaeological remains [52,53,54,55] were used to supporting our findings.

Historical accounts of ancient fisheries

Ichthyoarchaeological evidence and historical accounts from the Caribbean and tropical South America suggest that early prehistoric target species corresponded to the most accessible and vulnerable animals, such as sharks, large groupers [56,57,58], turtles [59,60] and sea mammals [61,62,63,64].

Colonial accounts from 1587 [56] on the semi-sedentary indigenous community that lived in Brazil during the early days of Portuguese colonization refer to the paleo-Indian fisheries' expertise and their use of rich marine food supplies; the accounts additionally demonstrate a traditional knowledge of fish diversity, reproductive aggregation of fish, fishery areas and environmental relationships. Regarding fish diversity, a list of the 43 most important species of fish was reported accurately (Table 1) [56]. These fish records are in agreement with the prehistoric data presented here. Most of the historic narrative regarding fish captures concerns reproductive periods in coastal and estuarine areas, where bony fishes form compact aggregations along the littoral zone during the intertidal phase. The account '*curiosi rerum naturae*' [56] refers to high marine fish abundance, especially during the summer on the coast of Salvador in the state of Bahia (northeast Brazil), when female bony fishes have large gonads. Additionally, the narrative talks about the 'docile and very easily caught giant grouper on the beaches', the large tarpon size, 'longer than an Indian is tall', and the 'thousands of mullet caught during a single day fishing', revealing a picture of the abundance of fishery resources [56,65]. All these historical narratives are in agreement with the fact that Brazilian neo-Indians were skilled fishermen, using arrows, marksmanship, and fishery lines with hooks; they built fish traps with wood and rocks in an intertidal beach and small nets for cooperative fisheries. These undeniable skills were possibly inherited from ancestral paleo-Indians who perfected the art of fishing [66].

Shellmounds are the best testimonial resource for understanding the paleo-Indian fishery activities. However, most of the original context of Brazilian shellmounds was destroyed due to the use of mollusk shells to produce lime and fertilizers for paving of roads and streets,

Table 1. Brazilian colonial fish records [56].

Indigenous names	Probable species	Fishery tool and remarks
aragoagoay	*Pristis* sp.	hooks and spear
uperu, panapaná, socorí	shark	hooks and spear
beijupirá	*Rachycentron canadum*	hooks
tapyrsiçá	*Seriola lalandi*	hooks
camuropi	*Megalops atlanticus*	hooks, very large
piraquiroá	*Selene* sp.	hooks
carapitanga	*Lutjanus* sp.	hooks
canapú	*Epinephelus itajara*	hooks, tides stones and sticks tramp, very large, easy capture
cupá	*Cynoscion* sp.	hooks
guaripicú	*Scomberomorus* sp.	trolling lines
guiará	*Chaetodipterus faber*	hooks and beach seine
guris and urutús	Ariidae	hooks
caramurú	*Echidna* sp.	hands
jabubirá	Dasyatidae or Myliobatidae	hooks and beach seine
tacupapirema	*Micropogonias furnieri* or *Cynoscion acoupa*	hooks
bonitos	Carangidae	hooks
dourada	*Coryphaena hippurus*	hooks
caraoatá	*Thunnus* sp.	hooks
garoupas	*Epinephelus* sp.	hooks, very large
camurîs	*Centropomus* sp.	hooks
abróteas	*Urophycis brasiliensis*	hooks
ubaranas	*Elops saurus*	hooks
goaivicoára	*Conodon nobilis*	hooks
sororocas	*Scomberomorus maculatus*	hooks
timaçu	*Strongylura* sp.	used for bait
miracoaia	*Stellifer* sp. or *Bairdiella* sp.	hooks
maracuguara	*Balistes* sp.	hooks
paratîs	*Mugil curema*	sticks tramp and net during high tide
zabucai	*Selene* sp.	beach seine
tareîra	*Caranx hippos*	beach seine
coirimás	*Mugil liza*	beach seine
arabori	*Brevoortia aurea*	beach seine
carapebas	*Eucinostomus* sp.	beach seine
jaguaraçá	*Holocentrus adscensionis*	hooks, medicinal
piraçaque	*Conger* sp.	hooks, medicinal
bodiaens	*Scarus* sp.	hooks, medicinal
atucupá	*Cynoscion* sp.	hooks, medicinal
goayibicoati	Gobiidae	hooks, medicinal
uramaçâ	Paralichthyidae	hooks, medicinal
baiacú	*Lagocephalus* sp.	fishes that producing poisoning
piraquiroâ	*Chilomycterus antillarum*	fishes that producing poisoning
aimoré	Gobiidae	fishes that producing poisoning

The first ichthyofaunal list (indigenous name) documented from the Brazilian coast.

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construction of forts, colonial houses, churches, among others applications. This occurred starting in 1549 in the area of Salvador, Bahia and other colonial settlements along the Brazilian coast and continued until the 1960s, when archaeological shellmounds became protected under Brazilian federal law.

Geographic setting

From south to north, the landscape of the Rio de Janeiro coast is characterized by the presence of a crystalline shield (Serra do Mar relief), with plenty of high (approximately 1,200 m) mountain scarps parallel to the Atlantic Ocean in the vicinity of Angra dos Reis [67]. The area is characterized by short rivers flowing to the coast and fluviomarine plains in an embayment (i.e., Ribeira Bay), a jagged coastline, with small peninsulas and several rocky islets [68]. The beaches and the sandy stretches are not developed, and the shellmounds are predominantly located over the rocky islets in an area dominated by mangrove flood plains. Small submarine channels approximately 6 to 10 m deep characterize the coastal bathymetry, and near Ilha Grande bay, the depth reaches approximately 30 m. Ilha Grande is a massive structural island with fairly rugged relief; it is isolated from the mainland by a channel approximately two kilometers wide.

The Itaipú-Camboinhas region is located on the oceanfront of Niterói and has sandy beaches dominated by dunes and sandy bars, which separate the sea from Piratininga and Itaipu coastal lagoons. The semicircular sandy beach has depths of approximately 3 to 16 m that extend almost 1,000 m offshore. The landscape has a mountainous relief aligned in the SW-NE direction [47]. The Camboinhas shellmound is located over a sand dune, near the coastal line and the tidal channel of Itaipu Lagoon.

The Saquarema region is located in a landscape characterized by a crystalline rock relief, which separates the two major drainage basins that feed the Saquarema lagoon complex [47,68]. The sandy shore is shallow but exposed to high-energy coastal wind and waves. The area has the highest concentration of shellmounds in Rio de Janeiro; they are distributed along the sandy coastal plain of the inland sandbanks, facing the lagoon (e.g., Beirada, Manitiba, Ponte do Girau and Saquarema shellmounds).

In Arraial do Cabo, the structural NE-SW trend is characterized by a metamorphic basement (i.e., Pontal de Atalaia), rising up to 172 m high, and the adjacent Cabo Frio Island, an igneous alkaline rock (syenite, trachyte and breccia) with altitudes of approximately 380 m [69]. The Usiminas shellmound is located in the Cabo Frio Island, 50 m above sea level, facing the coastal plain, where the water depth is approximately 5 m. In contrast, the oceanfront cliffs on the opposite coast reach 50 m in depth near the coastline. Additionally, the Ilha do Cabo Frio shellmound is located on a small sandy beach characterized by an active dune that faces towards the landscape, associated with the outcrop layers that overlap the Cabo Frio beach rock [65,70]. Part of the lower layer of this shellmound is located below sea level [29].

Materials and Methods

Selected shellmounds from the southeastern coast of Rio de Janeiro State, Brazil have three main features: **(1)**, the potential marine influence of the Cabo Frio upwelling system (i.e., seasonal oceanographic mixing of South Atlantic Central Water, Subtropical Shell Water and the Brazilian Current, increasing biological productivity); **(2)**, the marine environment (i.e., shallow waters, coastal lagoons and a rocky bottom); and **(3)**, coastal geomorphology (i.e., sandy coastal plains, rocky islands and rocky bays).

The shellmounds included in this study are the following: the Usiminas shellmound [71], on a rocky settlement, and the Ilha do Cabo Frio shellmound [72], on a sandy beach on Cabo

Frio Island (23°00' 18" S, 42°00' 20" W); Saquarema [72], Beirada [46], Manitiba [73] and Ponte do Girau [74] shellmounds, on a sandy coastal plain with coastal lagoons in the Saquarema lagoon complex (22°55' 66" S, 42°29' 00" W); Camboinhas shellmound [75], on a sandy coastal plain with coastal lagoons in the oceanic region of Niterói (22°57' 54" S, 44°02' 53" W); Algodão, Major, Bigode, Caieira and Peri shellmounds [76], on rocky islets and coastal rocky bays in the Ribeira Bay, Angra dos Reis (22°55' 48" S, 44°20' 48" W); and Acaiá shellmound (personal communication of an unpublished manuscript: Tenório, M.C. 'Os sambaquieiros e a gruta do Acaiá: Reconstituição do processo de formação de um sítio'), on a rocky island in the oceanfront of Ilha Grande (Fig 1).

We studied all the specimens deposited in the ichthyoarchaeological collection of Museu Nacional, Universidade Federal do Rio de Janeiro (MN-UFRJ), Rio de Janeiro, Brazil, and their use for this research was authorized by the collection managers, who are coauthors of this study (MCT and TL).

We have organized a referential species collection based on 679 diagnostic osteological and dental characters (details in S2 Appendix). Quantitative analyses of fish specimens and species recovered from each shellmound are necessary for accurate data interpretation. However, different archaeological methods were used in these shellmounds during excavation conducted by UFRJ archaeologists between 1981 and 2005. The methods included sieving techniques, removing material and curatorial processing. These and others questions regarding the repository, catalog and samples labels will require more detailed assessment, which is beyond of the scope of this study. Consequently, the fish diversity analyzed here is based on a qualitative study and the frequencies of species by shellmound.

All relevant specific characteristics of examined species were identified based on comparative anatomy, using 39 shark and ray specimens (among teeth, vertebrae and spines) housed at the Universidade Estadual do Rio de Janeiro (UERJ) and using at least 115 otoliths and 21 dry finfish individual skeletons housed at the Universidade Federal Fluminense (UFF) (details in S3 Appendix). All structures are in a good state of conservation and relevant specific osteological characteristics were also identified based on extensive bibliographic review.

Photographs of the otoliths were taken with a Leica M205A multifocal stereomicroscope. Photographs of bones, sharks and rays teeth were taken using a digital microscope and digital camera. A complete atlas of the most common diagnostic teeth, otoliths and bones recovered and observed from shellmound collections is included in the plates of the present paper.

Cluster analysis was performed under the Paleontological Statistics Software (PAST, version 2.17c) on Q-mode (i.e., grouping variables) to analyze shellmound similarity patterns. This exploratory technique identifies the relationships and patterns among multiple variables across samples and has been applied in a wide range of scientific fields, such as marine and fisheries ecology [77,78,79,80]. The analysis was based on the presence and absence of fish assemblages in the shellmounds, archaeological site ages, littoral geomorphology and prehistoric fisheries. The unweighted pair-group average (UPGMA) algorithm was used with the Bray-Curtis similarity-association matrix of [81].

Estimates of shark-body total length (TL) were based on 660 isolated vertebrae, using a unique linear regression equation for each species: *Carcharias taurus* TL = 36.786 +10.753 CR [82], *Sphyrna lewini* TL = 4.51 + 23.64 CR [83], *Carcharhinus brevipinna* CD = 0.0159 PCL– 0.1285, PCL = 0.799 TL– 9.07 [84] and *Carcharodon carcharias* FL = 21+ 11.8 CR, FL = 0.94 TL– 5.74 [85], where TL is the total length, FL is the fork length, PCL the precaudal length, CD the vertebral centrum diameter and CR the vertebral centrum radius.

The main teleostean fish target, based on the frequency observed in the shellmounds, was the whitemouth croaker, *Micropogonias furnieri* [86], which was present in all shellmounds with the exception of the Usiminas and Ilha do Cabo Frio shellmounds, both on Cabo Frio

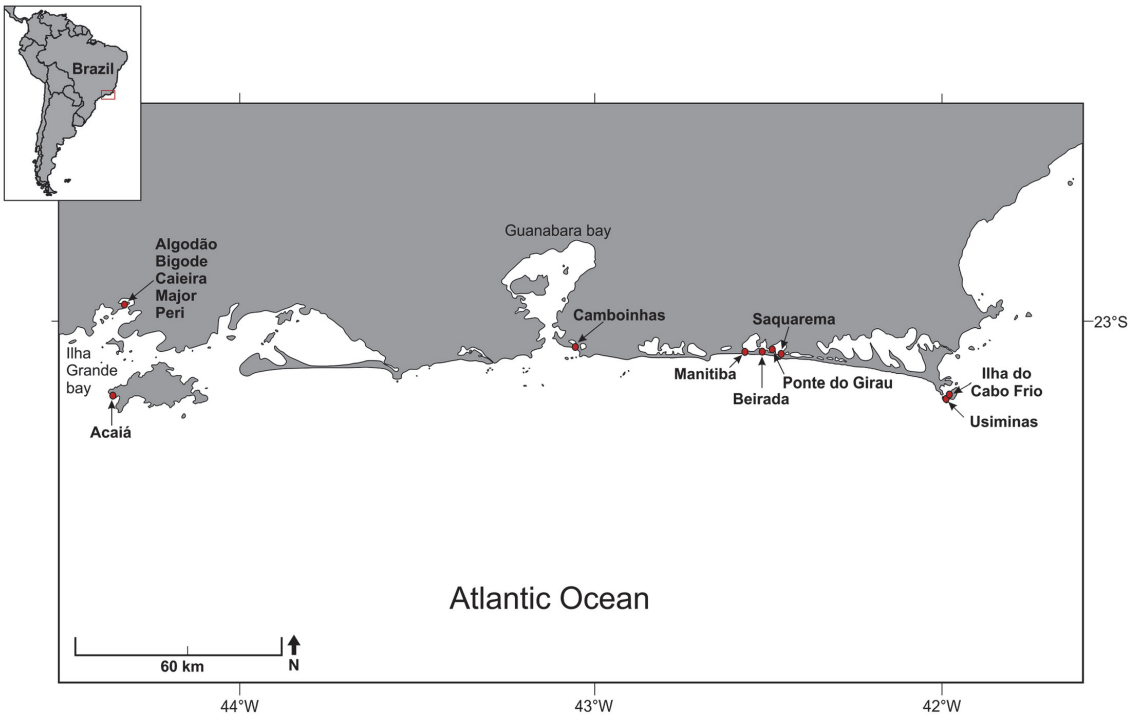

Fig 1. Study area along the southeastern Brazilian coast showing shellmound locations.

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Island. The life history of *M. furnieri* in the Western Atlantic Ocean is well known [87,88], and they can be found in commercial [89,90] and local artisanal fisheries [77,91]. We used this species to interpret and compare changes between past and present coastal fisheries on the southeastern Brazilian coast. We tested for differences between the medians of length frequency distributions (Student's t-test, PAST software v. 3.7) after checking for normality and homogeneity of variances.

A total of 5,532 archaeological whitemouth croaker, *Micropogonias furnieri*, otoliths were measured using digital callipers. These specimens were distributed among the shellmounds as follows: Ponte do Girau (376 specimens), Beirada (2,541 specimens), Manitiba (1,372 specimens), Algodão (1,148 specimens) and Camboinhas (95 specimens). Fish total lengths (TL) were calculated based on the archaeological otolith total length (OL) using the following equation, which we derived from a regression analysis: TL = 24.34 + 22.57 OL (r = 0.988, n = 93). To compare the estimates of body size length data between shellmound samples, we performed a nonparametric variance analysis of medians (Kruskal-Wallis test) and an *a posteriori* test of the shellmound context, analyzing the localities and related environmental factors using the free software R [92].

We chose not to use the South American Western Atlantic fish records [88]; instead, specific references of modern fish diversity and abundance in the littoral areas close to the shellmounds

of Rio de Janeiro were obtained from Arraial do Cabo [58,93,94], Itaipu [77,95] and Ribeira Bay in Angra dos Reis [96], and these were used in comparisons with fishery records.

Data from the Brazilian fishery survey of whitemouth croaker in the Itaipu modern fisheries (i.e., artisanal and semi-industrial) are based on records compiled between 2000 and 2004 [77] from the Angra dos Reis Bay from semi-industrial fisheries captures reported between 2013 and 2014. At Guanabara Bay, a fishery study was conducted using a bottom trawl between 2005 and 2007 [91].

The samples for radiochronology were prepared and analyzed at the Radiocarbon Laboratory of the Universidade Federal Fluminense (LAC-UFF). The otolith samples were chemically treated with HCl and converted to CO_2 by hydrolysis with H_3PO_4. Graphitized samples were placed in the 40-sample wheel of the SNICS ion source and measured in an NEC 250 kV Single Stage Accelerator System (SSAMS) [97]. Typical currents were 50 $\mu A^{12}C^{-1}$ (measured at the low energy Faraday cup). Graphite standard and calcite blanks yielded average $^{14}C/^{13}C$ ratios of 6 $x10^{-13}$ and $7x10^{-13}$, respectively. The average machine background was approximately 50 kHz for the unprocessed graphite, while the average precision ranged from 0.3 to 0.5%. Data analyses were carried out on LACAMS software developed at the Physics Institute of Universidade Federal Fluminense [98]. Calibration of otolith radiocarbon dates was performed with OxCal software v 4.2.3 from the Oxford University [99], using the Marine13 curve [100] in the 2-sigma range with an offset for local marine reservoir corrections (ΔR ^{14}C years) according to the following shellmound localities: Saquarema [53], Manitiba [55] and Southeastern Brazil [101]. Cross-comparisons were conducted in the Beta Analytic Inc. laboratory, following standard protocols.

We exclusively used the fish otolith radiocarbon dates to determine ages for chronological interpretation of the fish assemblages of most shellmounds, except for those from the Cabo Frio Island, where otoliths of whitemouth croaker could not be recovered; additionally, a few otoliths from Ilha Grande could not be dated. Consequently, we refer only to ages that were not derived from otolith samples for the Usiminas, Ilha do Cabo Frio and Acaiá shellmounds. The age ranges of those sites are based on charcoal and shell data ([29,102]; personal communication).

Results

Shellmound radiocarbon dating based on otoliths and the identified fish assemblages are shown in Table 2. Manitiba serves as an example of a multilayer shellmound (i.e., seven archaeostratigraphic layers in 2.2 m of depth) and demonstrates the difficulty in distinguishing radiocarbon age differences between successive layers; here, the calibration curve associated with the error bar and the reservoir effect cause the age range to overlap (Fig 2). This inhibits inferring a chronological sequence for fisheries in shallow shellmounds. We, therefore, use individual shellmound dating as a marker of settlement period.

A total of 97 fish species have been identified from the Rio de Janeiro shellmounds, representing 37% of the total (265 spp.) modern species recorded from the Rio de Janeiro coast [e.g., Arraial do Cabo (135 spp.), Itaipu (165 spp.) and Angra dos Reis (139 spp.)]. Table 2 shows the occurrence in archaeological sites of the great white shark, *Carcharodon carcharias*, the sand tiger shark, *Carcharias taurus*, the porbeagle shark, *Lamna nasus*, the lemon shark, *Negaprion brevirostris*, the tiger shark, *Galeocerdo cuvier*, and a large diversity of other sharks (such as Carcharhinidae, Sphyrnidae, and other coastal species) in the rocky islet shellmounds of Angra dos Reis (Ribeira Bay: Algodão, Bigode, Caieira, Major and Peri sites), Ilha Grande (Acaiá) and Cabo Frio Island (Usiminas and Ilha do Cabo Frio). The data also include the occurrence of other rarer shark species found in the shellmounds located over sandy coasts and coastal

Table 2. Ichthyoarchaeological records from the Rio de Janeiro shellmounds (Saquarema, Cabo Frio, Niterói, Ilha Grande and Angra dos Reis).

Region		SAQUAREMA				NITERÓI	ANGRA DOS REIS						ILHA GRANDE	ILHA DO CABO FRIO			
Shellmounds		Beirada	Saquarema	Manitiba	Girau	Camboinhas	Algodão	Bigode	Caieira	Peri	Major		Acaiá	Usiminas	Ilha do Cabo Frio	Structures	Figures
Geomorphology		Sandy coastal plain and coastal lagoons				Sandy beach	Rocky bottom and rocky islet						Rocky island		Sandy beach		
Radiocarbon age ranges		3035 to 5595 cal BP	2100 to 4200 cal BP	3695 to 4515 cal BP	3730 to 4525 cal BP	4160 to 4960 cal BP	2345 to 4414 cal BP	3223 to 3525 cal BP	1875 to 2175 cal BP	890 to 1140 cal BP	675 to 900 cal BP		2760 to 2930 cal BP*	1265 to 1765 cal BP*	2710 to 3290 cal BP*		
Chondrichthyes																	
Odontaspididae	*Carcharias taurus*			•		•	•	•	•	•	•		•	•	•	teeth, vertebrae	Fig. 8.1; 10.1; 10.4
Alopidae	*Alopias superciliosus*		•													teeth	Fig. 8.2
Lamnidae	*Carcharodon carcharias*	•	•			•	•			•	•		•	•	•	teeth, vertebrae	Fig. 7.1; 8.3; 10.2; 10.3
	Isurus oxyrinchus						•	•	•	•	•		•	•	•	teeth	Fig. 8.4
	Lamna nasus						•	•	•	•	•			•	•	teeth	Fig. 8.5
Carcharhinidae	*Carcharhinus acronotus*						•		•		•				•	teeth	Fig. 8.6
	Carcharhinus altimus												•			teeth	Fig. 7.2
	Carcharhinus brevipinna	•	•			•	•						•	•	•	vertebrae	Fig. 10.5-10.7
	Carcharhinus leucas														•	teeth	Fig. 7.3
	Carcharhinus limbatus						•	•	•	•	•		•			teeth	Fig.8.8
	Carcharhinus obscurus	•	•										•			teeth.	
	Carcharhinus plumbeus	•					•		•	•	•			•		teeth	Fig.7.4; 8.9
	Carcharhinus porosus						•	•	•	•	•					teeth	
	Carcharhinus priscus										•			•	•	teeth	
	Carcharhinus sp.	•	•			•	•						•	•	•	teeth	Fig. 10.8; 10.10-10.12
	Galeocerdo cuvier						•		•	•	•		•	•	•	teeth	Fig. 7.5; 8.10
	Negaprion brevirostris		•				•	•	•	•	•		•		•	teeth	Fig. 8.11
	Rhizoprionodon lalandii						•	•		•	•					teeth	Fig. 8.12
	Rhizoprionodon porosus						•	•			•					teeth	Fig. 8.14

(*Continued*)

Table 2. (*Continued*)

Region		SAQUAREMA			NITEROI	ANGRA DOS REIS					ILHA GRANDE	ILHA DO CABO FRIO			
Shellmounds		Beirada	Saquarema	Manitiba	Girau	Camboinhas	Algodão	Bigode	Caleira	Peri	Major	Acaiá	Usiminas	Ilha do Cabo Frio Sandy beach	Structures	Figures
Geomorphology		Sandy coastal plain and coastal lagoons				Sandy beach	Rocky bottom and rocky islet					Rocky island				
Radiocarbon age ranges		3035 to 5595 cal BP	2100 to 4200 cal BP	3695 to 4515 cal BP	3730 to 4525 cal BP	4160 to 4960 cal BP	2345 to 4414 cal BP	3223 to 3525 cal BP	1875 to 2175 cal BP	890 to 1140 cal BP	675 to 900 cal BP	2760 to 2930 cal BP*	1265 to 1765 cal BP*	2710 to 3290 cal BP*		
	Rhizoprionodon sp.												•		vertebrae	Fig. 10.9
Sphyrnidae	*Sphyrna mokarran*		•				•		•		•				teeth	Fig. 7.6; 8.7; 8.15
	Sphyrna zygaena						•				•		•		teeth	Fig. 8.16
	Sphyrna sp.					•			•	•		•	•		teeth, vert.	Fig. 10.13; 10.14
Pristidae	*Pristis* sp.		•				•					•	•		vertebrae	Fig. 9.1; 9.2
Dasyatidae	*Dasyatis centroura*	•	•			•									caudal spine	Fig. 9.6
Myliobatidae	*Aetobatus narinari*					•	•					•	•	•	tooth	Fig. 9.7
Rhinopteridae	*Rhinoptera* sp.						•					•		•	tooth	Fig. 9.3; 9.4
	Osteichthyes															
Albulidae	*Albula nemoptera*						•								otolith	Fig. 11.1
Ariidae	*Aspistor* sp.			•											bones	Fig. 13.1
	Bagre bagre						•				•				otolith	
	Bagre marinus						•	•		•		•			otolith, bones	Fig. 11.2; 13.2
	Bagres sp.			•											bones	
	Cathorops sp.			•											bones	Fig. 13.3
	Genidens genidens			•		•						•			otolith, bone	Fig. 11.3
	Genidens barbus			•											bones	Fig. 13.4
	Genidens sp.			•											bones	Fig. 13.5-13.8
	gen. sp. ind.				•								•		otolith	
Hemiramphidae	*Hemiramphus* sp.								•						otolith	Fig. 11.4; 11.5
Holocentridae	*Sargocentrum* sp.											•			bones	Fig. 13.9
Centropomidae	*Centropomus* sp.											•	•		bones	
	Centropomus ensiferus						•				•			•	otolith	Fig. 11.6
	Centropomus undecimalis						•						•		otolith, bones	Fig. 11.7; 13.11
	Centropomus parallelus			•									•		bones	Fig. 13.10
Serranidae	*Epinephelus morio*						•								otolith	

(*Continued*)

Table 2. (*Continued*)

Region		SAQUAREMA			NITEROI	ANGRA DOS REIS					ILHA GRANDE	ILHA DO CABO FRIO			
Shellmounds		Beirada	Saquarema	Manitiba	Girau	Camboinhas	Algodão	Bigode	Caleira	Peri	Major	Acaiá	Usiminas	Ilha do Cabo Frio	Structures	Figures
Geomorphology		Sandy coastal plain and coastal lagoons				Sandy beach	Rocky bottom and rocky islet					Rocky island		Sandy beach		
Radiocarbon age ranges		3035 to 5595 cal BP	2100 to 4200 cal BP	3695 to 4515 cal BP	3730 to 4525 cal BP	4160 to 4960 cal BP	2345 to 4414 cal BP	3223 to 3525 cal BP	1875 to 2175 cal BP	890 to 1140 cal BP	675 to 900 cal BP	2760 to 2930 cal BP*	1265 to 1765 cal BP*	2710 to 3290 cal BP*		
	Epinephelus marginatus												•		otolith	Fig. 11.9
	Epinephelus sp.						•				•	•	•	•	otolith, bones	Fig. 11.3; 13.12; 13.13
	Mycteroperca sp.												•		bones	Fig. 13.14
Coryphaenidae	*Coryphaena hippurus*											•			bones	
Carangidae	*Caranx hippos*					•						•	•		bones	
	Caranx sp.		•			•						•			bones	Fig. 13.15; 13.16
	Oligoplites saurus											•			bones	Fig. 14.1
	Selar crumenophthalmus											•			bones	
	Selene vomer											•	•		bones	Fig. 13.17; 13.18
Lutjanidae	*Lutjanus synagris*						•	•	•	•	•				otolith	Fig. 11.10
	Lutjanus sp.						•	•	•		•			•	otolith	Fig. 11.11
	Ocyurus chrysurus												•		otolith	Fig.11.12
	gen., sp. ind.													•	bones	
Gerreidae	*Diapterus rhombeus*						•		•	•	•				otolith	Fig. 11.13
	Gerres cinereus						•								otolith	Fig. 11.16
	gen., sp. ind.						•		•		•				bones	Fig. 14.3
Haemulidae	*Anisostremus virginicus*						•	•	•	•	•		•		otolith	Fig. 11.17
	Anisostremus sp.						•								bones	Fig. 14.4; 14.5
	Haemulon aurolineatum						•						•		otolith	Fig. 11.18
	Haemulon sciurus						•								otolith	Fig. 11.19
	Haemulon steindachneri						•		•				•		otolith	Fig. 11.20
	Haemulon sp.									•	•				otolith	
	Orthopristis ruber								•		•				otolith	
Sparidae	*Archosargus rhomboidalis*						•				•				otolith	Fig. 11.21

(*Continued*)

Table 2. (*Continued*)

Region		SAQUAREMA			NITEROI	ANGRA DOS REIS					ILHA GRANDE	ILHA DO CABO FRIO			
Shellmounds		Beirada	Saquarema	Manitiba	Girau	Camboinhas	Algodão	Bigode	Caleira	Peri	Major	Acaiá	Usiminas	Ilha do Cabo Frio Sandy beach	Structures	Figures
Geomorphology		Sandy coastal plain and coastal lagoons				Sandy beach	Rocky bottom and rocky islet					Rocky island				
Radiocarbon age ranges		3035 to 5595 cal BP	2100 to 4200 cal BP	3695 to 4515 cal BP	3730 to 4525 cal BP	4160 to 4960 cal BP	2345 to 4414 cal BP	3223 to 3525 cal BP	1875 to 2175 cal BP	890 to 1140 cal BP	675 to 900 cal BP	2760 to 2930 cal BP*	1265 to 1765 cal BP*	2710 to 3290 cal BP*		
	Archosargus sp.						•					•		•	otolith, bones	Fig. 11.22; 14.7
	Diplodus sp.						•				•	•			otolith, bones	Fig. 11.14; 11.15; 14.6
	Pagrus pagrus												•		bones	
Sciaenidae	*Bairdiella ronchus*						•	•	•						otolith	Fig. 11.23
	Cynoscion acoupa		•												otolith	Fig. 11.26
	Cynoscion jamaicensis											•			otolith	Fig. 11.24
	Cynoscion microlepidotus				•		•	•	•	•	•				otolith	Fig. 11.25
	Larimus breviceps						•		•						otolith	Fig. 11.27
	Micropogonias furnieri	•	•	•	•	•	•	•	•	•	•	•			otolith, bones	Fig. 11.28
	Pareques acuminatus			•											otolith	Fig. 11.29
	Pogonias cromis	•	•	•	•		•							•	otolith, bones	Fig. 12.1; 14.9
	Umbrina coroides													•	otolith	Fig. 12.2
Mugilidae	*Mugil liza*						•	•	•	•	•				otolith	Fig. 12.3
	Mugil sp.			•											bones	Fig. 14.10
Labridae	*Bodianus rufus*											•		•	bones	Fig. 14.11; 14.12
Scaridae	*Scarus* sp.						•					•		•	bones	Fig. 14.14; 15.1; 15.2; 15.5
	Sparisoma sp.											•	•	•	bones	Fig. 14.3; 14.13; 15.3;15.4; 15.13
Trichiuridae	*Trichiurus lepturus*											•			bones	Fig. 15.6
Scombridae	*Katsuwonus pelamis*											•	•	•	bones	Fig. 15.7; 15.8
	Scomberomorus sp.											•	•		bones	Fig. 15.9
Istiophoridae	*Istiophorus albicans*											•	•		bones	Fig. 15.10

(*Continued*)

Table 2. (*Continued*)

Region		SAQUAREMA				NITEROI	ANGRA DOS REIS					ILHA GRANDE	ILHA DO CABO FRIO			
Shellmounds		Beirada	Saquarema	Manitiba	Girau	Camboinhas	Algodão	Bigode	Caieira	Peri	Major	Acaiá	Usiminas	Ilha do Cabo Frio	Structures	Figures
Geomorphology		Sandy coastal plain and coastal lagoons				Sandy beach	Rocky bottom and rocky islet					Rocky island		Sandy beach		
Radiocarbon age ranges		3035 to 5595 cal BP	2100 to 4200 cal BP	3695 to 4515 cal BP	3730 to 4525 cal BP	4160 to 4960 cal BP	2345 to 4414 cal BP	3223 to 3525 cal BP	1875 to 2175 cal BP	890 to 1140 cal BP	675 to 900 cal BP	2760 to 2930 cal BP*	1265 to 1765 cal BP*	2710 to 3290 cal BP*		
Ephippidae	*Chaetodipterus faber*		•										•		bones	
Sphyraenidae	*Sphyraena barracuda*												•		bones	Fig. 15.11
	Sphyraena guachancho						•				•				otolith	Fig. 12.4
	Sphyraena sp.								•		•	•	•	•	otolith, bones	
Hyporhamphidae	*Hyporhamphus unifasciatus*						•		•						otolith	Fig. 12.5
Tetraodontidae	*Lagocephalus laevigatus*						•					•		•	bones	Fig. 15.12
Diodontidae	*Chilomycterus spinosus*						•								bones	Fig. 15.15
	Diodon sp.												•		bones	Fig. 15.14

Ages are based on radiocarbon analyses of otoliths (*M. furnieri*). Ages with asterisks indicate that otolith radiocarbons ages were not available and charcoal- and shell-derived ages were used instead ([29,102]; personal communication).

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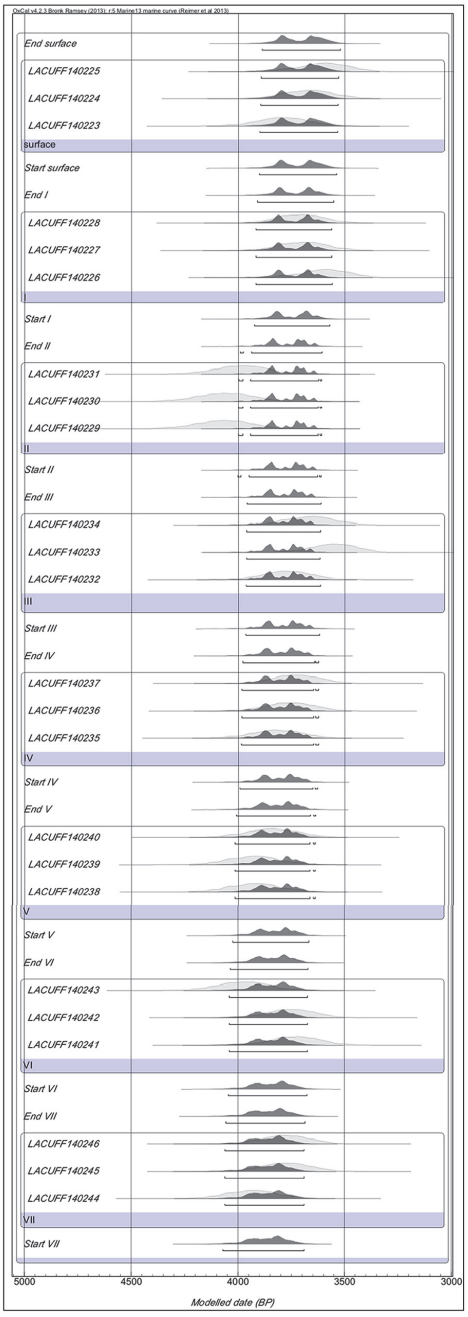

Fig 2. Modeled age based on whitemouth croaker otolith samples from multiple archaeological layers of Manitiba in Saquarema using OxCal v 4.2.3 [99]. This figure shows ages obtained by radiochronology (vertical lines). The error bar, represented by the horizontal line, shows a range of ages that spans

approximately 370 years across the seven archaeostratigraphic sections, hindering a precise dating of the layers.

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lagoons. These remains (i.e., shark teeth and vertebrae) have been recovered in 100% of the analyzed shellmound samples, especially from those associated with rocky islands and islets. The remains of the spotted eagle ray, *Aetobatus narinari*, were the most frequent from the ray group (batoids). The frequency of bony fish remains suggest that some species of groundfish, inhabitants of sandy and muddy bottom or rocky spots, such as croakers (Sciaenidae), snappers (Lutjanidae), grunts (Haemulidae), groupers (Serranidae) and snooks (Centropomidae), were common target species. Sea catfish (Ariidae) and mullet (Mugilidae) species were frequent in localities with sandy and muddy bottoms associated with coastal lagoons. Rocky reef fishes, which are mostly durophagous (i.e., feeding on mollusks, echinoids and crabs), are represented by species of parrotfish (Scaridae), pufferfish (Tetraodontidae) and porcupinefish (Diodontidae), and their remains were particularly frequent in localities associated with rocky islands. Pelagic fish, including bluefish (Pomatomidae), sailfish (Istiophoridae), dolphinfish (Coryphaenidae), jacks (Carangidae), mackerel and tuna (Scombridae), were frequent in the shellmounds located in coastal and rocky islands oceanfront areas.

Based on the analyzed fish assemblages from shellmounds in Rio de Janeiro State, the nearshore fishery remains analyzed here were deposited 5,595 cal BP in the lagoon region of Saquarema and in the oceanfront region of Niterói (Fig 3, black circles). They were characterized by catches of coastal species associated with sandy bottoms and coastal lagoons. The fish could be accessible using beach seines during reproductive aggregation and spawning. These schools of fish include croaker, drum, catfish, mullet and snook. Later, approximately 4,414 cal BP, fishery activity records suggest a targeting of pelagic resources in protected rocky bays and around coastal rocky islets (Fig 3, black triangle). Rocky reef fishes were also a common target, and advances in artisanal fishery and multi-gear techniques remained successful until colonial times. At least since 3,290 cal BP, the fish assemblage recovery from the shellmounds located on the oceanic islands of Cabo Frio and Ilha Grande (Fig 3, black square) suggests a clear predominance of pelagic fisheries and a secondary use of rocky reef species.

The estimation of shark body size (TL) (Table 3) indicates that the spinner shark, *Carcharhinus brevipinna*, ranged from 44.3 to 263.1 cm; the sand tiger shark, *Carcharias taurus*, ranged from 79.3 to 192.2 cm; unidentified shark species of the genus *Carcharhinus* ranged from 38.8 to 115.1 cm; the hammerhead shark, *Sphyrna* sp., ranged from 10.1 to 40.0 cm; and the great white shark, *Carcharodon carcharias*, ranged from 88.2 to 249.6 cm.

Estimation of the body size distribution of whitemouth croaker, *Micropogonias furnieri* [range: 17.8 to 84.8 cm TL in all shellmounds (mean length ± SD: 43.3 ± 9.9 cm)]. These ichthyoarchaeological data overlap the modern size distributions from modern fisheries in Itaipu and Angra dos Reis in Rio de Janeiro State (Fig 4). However, the body size distribution of whitemouth croaker catches from prehistoric fisheries shows a probabilistic tendency toward higher frequencies of large specimens, resulting in an estimated 28% reduction in body size based on modern catches.

The results of ANOVA analyses (Kruskal-Wallis) on the median body sizes of whitemouth croaker show that, among the localities (Chi-squared = 1,042.3; df = 4, p values < 0.05), Beirada and Ponte do Girau shellmounds have significant similarities, and both are significantly different from other localities based on an *a posteriori* test (p values < 0.05). The comparative values of median body sizes from various environments and coastal geomorphologies (Chi-squared = 965.4, df = 2, p values < 0.05) reveal significant differences based on *a posteriori* tests (p values < 0.05) (Fig 5).

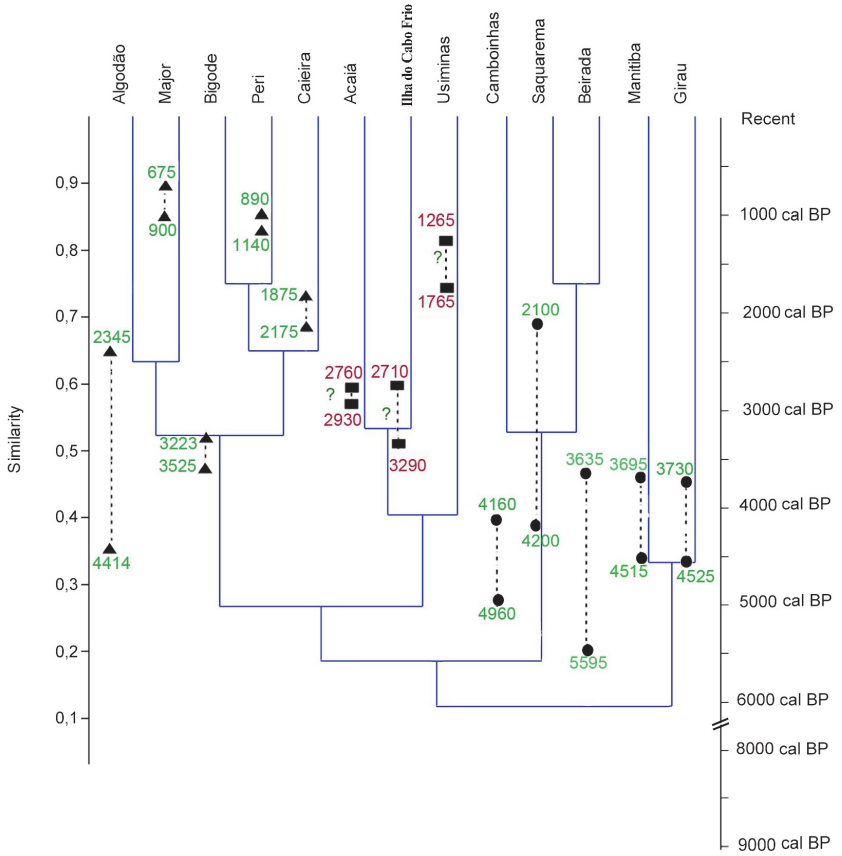

Fig 3. Cluster analysis of shellmound similarities. Age ranges (green letters) based on otolith data. Calibration was performed using Marine13 [100] in the 2-sigma range. The overall ΔR was found to be -56.5 to 120.5 [101]. The results at specific sites are as follows: ΔR Saquarema: -272 to -8 [53] and ΔR Manitiba: -224 to 60 [55]. Question marks indicate that radiocarbon dating of otoliths was not available; consequently, we plot shellmound age ranges (red numbers) based on charcoal and shell analyses ([29,102]; personal communication).

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The overlap of age ranges between the sequence of archaeological layers (Fig 2) dismisses the multilayer interpretation of the body size distribution in a given shellmound, and we use the Manitiba shellmound as the best example of this. However, the median body sizes of white-mouth croakers in different layers of the Manitiba shellmound show different values and an apparent tendency toward cyclicity of medians from the archaeological surface layer toward deeper layers. This could be interpreted as the result of seasonal oscillations in the intensity of the seasonal marine coastal upwelling (Fig 6).

Individual drilled shark teeth included *Carcharodon carcharias*, *Carcharhinus altimus*, *C. leucas*, *C. plumbeus*, *Galeocerdo cuvier* and *Sphyrna mokarran* (Fig 7). The biodiversity of fish

Table 3. Summary of shark species and body size data recorded from the Rio de Janeiro shellmounds.

Common name	Species	N	Shellmound localities	Body size range (cm)	Mean Size (cm)
Spinner shark	*Carcharhinus brevipinna*	500	ALG, CAM, USI	44.3–263.1	124.1 ± 55.1
Shark	*Carcharhinus* sp.	87	USI	38.8–115.1	64.6 ± 15.1
Great white shark	*Carcharodon carcharias*	12	ALG, CAM, USI	88.2–249.6	153.3 ± 58.2
Sand tiger shark	*Carcharias taurus*	12	ALG, CAM, USI	79.3–192.2	122.1 ± 31.2
Hammerthead	*Shyrpna* sp.	49	ALG, CAM, USI	10.1–40.0	20.2 ± 5.1

(N) Number of ichthyoarchaeological remains of vertebrae. Shellmound localities: (ALG) Algodão, (CAM) Camboinhas, (USI) Usiminas.

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fauna records was illustrated based on individual diagnostic structures (i.e., otoliths, teeth or bones remains) from the recovered specimens (Figs 8–15).

Discussion

We recognized 97 fish species from the Rio de Janeiro shellmounds based on detailed anatomic analysis of diagnostic structures. However, some taxonomic records (i.e., at least 44 taxa) that were previously cited in technical reports and unpublished theses about the Rio de Janeiro shellmounds could not be located in the MN-UFRJ repository for identification. These unexamined species are not under institutional catalogue records, and their descriptions or illustrations are not available. We, therefore, choose to exclude those 'specimens' from our analysis.

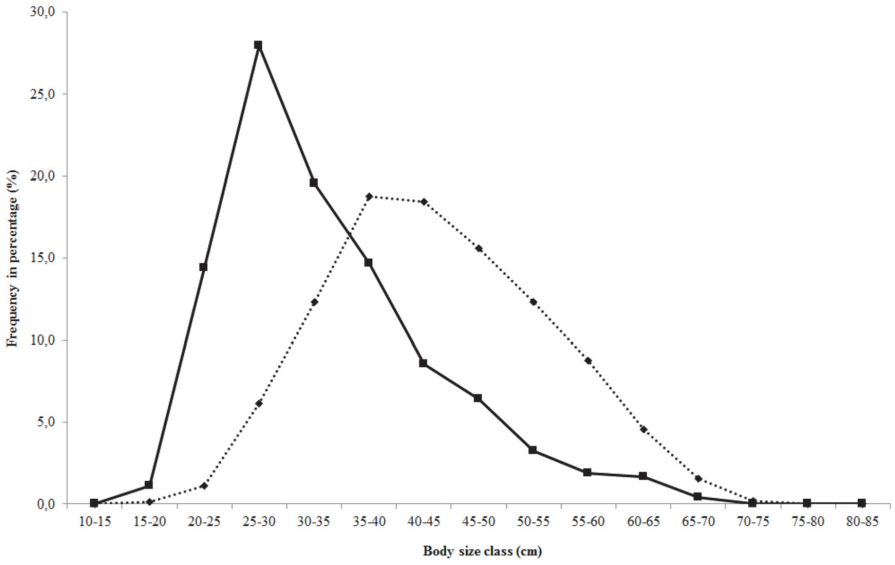

Fig 4. Frequency of body size classes of whitemouth croaker, *M. furnieri*. Ichthyoarchaeological (dashed line, N = 5,532) and modern fisheries (solid line, N = 3,914).

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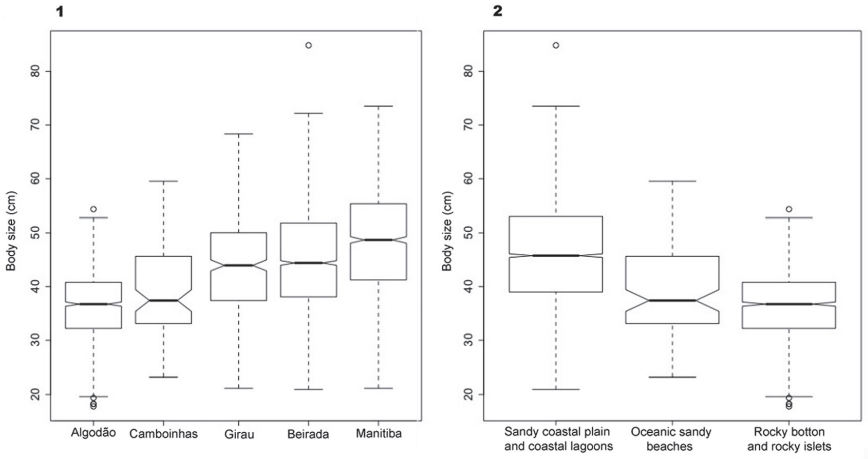

Fig 5. ANOVA analyses (Kruskal-Wallis) of medians based on estimates of body size classes of ichthyoarchaeological otoliths of *Micropogonias furnieri*, using R software (R Core Team 2012). (1) *A posteriori* test of body size medians versus shellmound localities. (2) *A posteriori* test of body size medians versus paleoenvironments where the shellmounds are located.

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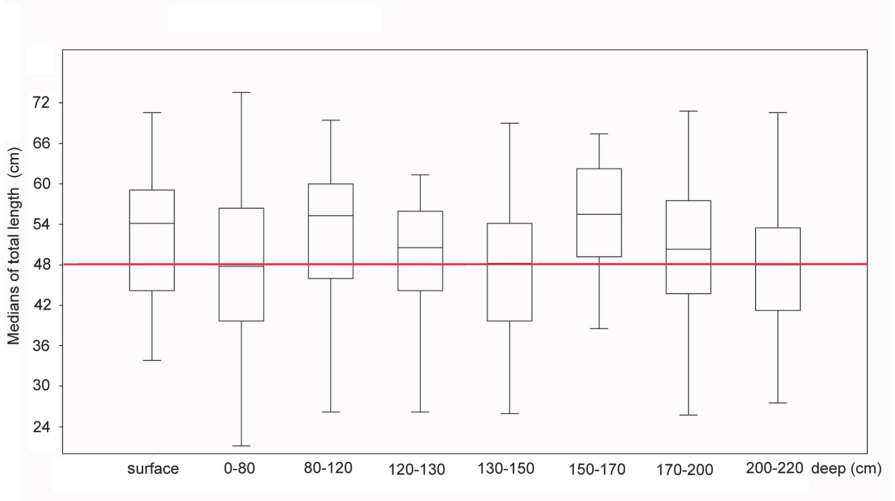

Fig 6. Comparative analyses of body size medians of whitemouth croaker from the multiple archaeological layers in the Manitiba shellmound in the Saquarema region. Note the differences among the layers, from the surface to deeper layers, and the trend of apparent cyclicity. The red line indicates the median of the total data set.

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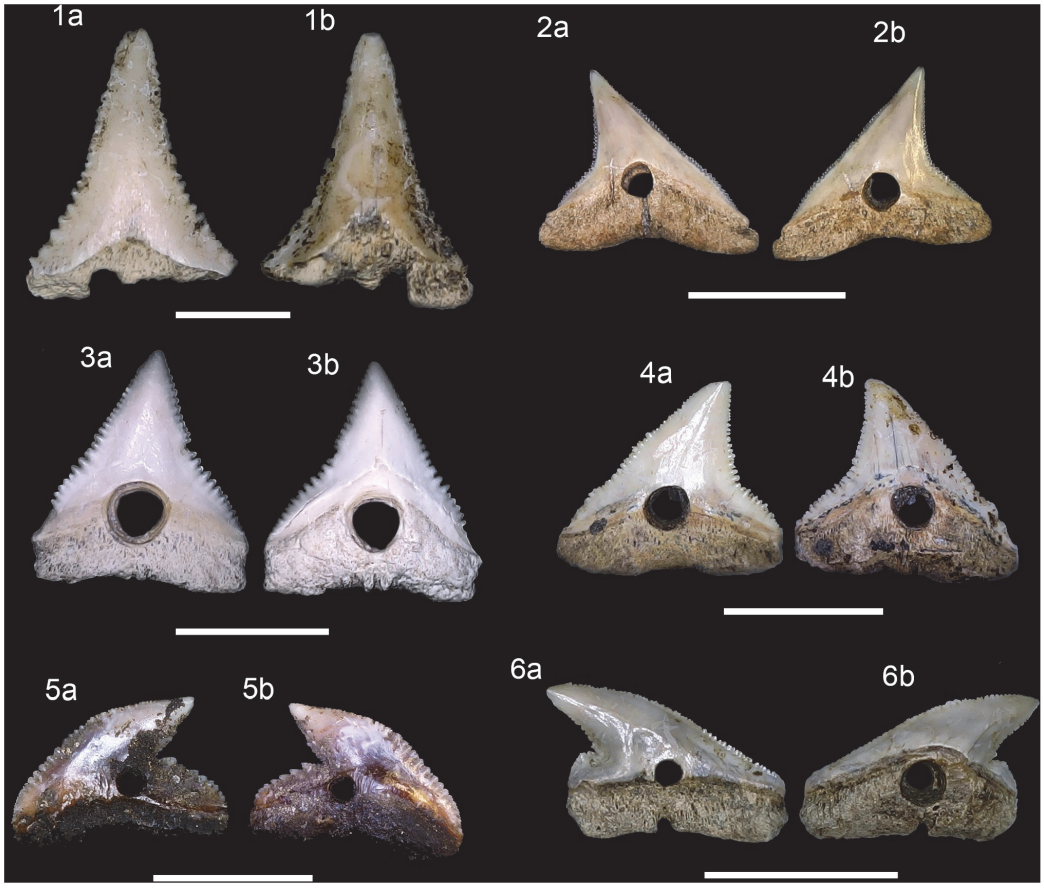

Fig 7. Drilled shark teeth. (1a-b) *Carcharodon carcharias*, lower tooth, Major, MNUFRJ-ZA-146. (2a-b) *Carcharhinus altimus*, upper tooth, Acaiá, MNUFRJ-ZA-868. (3a-b) *Carcharhinus leucas*, upper tooth, Ilha do Cabo Frio, MNUFRJ-ZA-869. (4a-b) *Carcharhinus plumbeus*, upper tooth, Caieira, MNUFRJ-ZA-97. (5a-b) *Galeocerdo cuvier*, indet. position tooth, Acaiá, MNUFRJ-ZA-870. (6a-b) *Sphyrna mokarran*, upper tooth, Algodão, MNUFRJ-ZA-54. Scale bar 1 cm.

doi:10.1371/journal.pone.0154476.g007

Population structures from shellmounds suggest that the estimated body length of coastal species (e.g., carcharhinids) follows a common pattern of juvenile and adult body length. Moreover, very small teeth and vertebrae of lamnids and sphyrnids collected from the shellmounds of Angra dos Reis and Cabo Frio Island indicate the possible presence of pregnant females, neonates and juveniles in a protected coastal area. Similar evidence is provided by large and very small vertebrae of sawfishes, *Pristis* spp. (Fig 9).

The *Carcharhinus brevipinna* size estimation is in agreement with the common length of contemporary specimens (i.e., 250 cm TL [71]), and the species is classified as a threatened species [103]. The estimated sizes of *Carcharias taurus* are two times smaller than those of their living counterpart (i.e., 250 cm TL [71]), which is classified as a vulnerable species [104]. Juvenile sizes of *Carcharhinus* species coincide with the most common length of the living

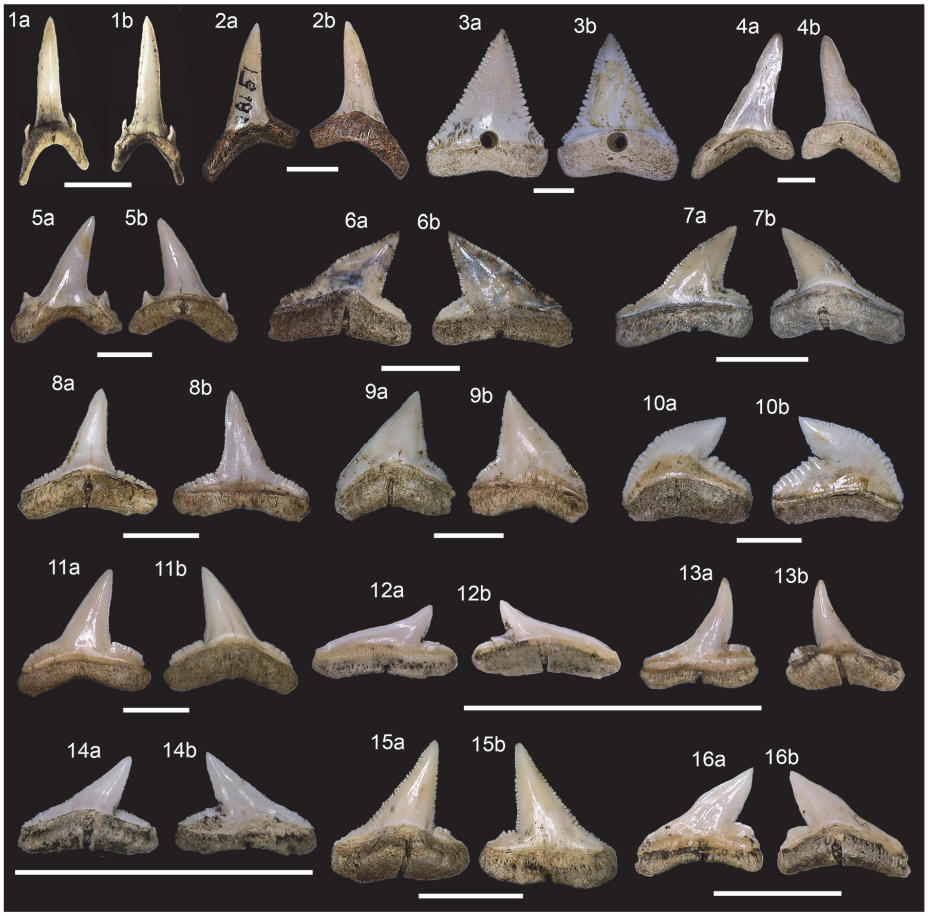

Fig 8. Shark teeth from Rio de Janeiro shellmounds. (1a-b) *Carcharias taurus*, upper tooth, Usiminas, MNUFRJ-ZA-565. (2a-b) *Alopias superciliosus*, upper tooth, Saquarema, MNUFRJ-ZA-Col.L.Kneip 28151. (3a-b) *Carcharodon carcharias*, upper tooth, Algodão, MNUFRJ-ZA-02. (4a-b) *Isurus oxyrinchus*, upper tooth, Algodão, MNUFRJ-ZA-21. (5a-b) *Lamna nasus*, lower tooth, Algodão, MNUFRJ-ZA-16. (6a-b) *Carcharhinus acronotus*, upper tooth, Algodão, MNUFRJ-ZA-01. (7a-b) *Sphyrna mokarran*, lower tooth, Major, MNUFRJ-ZA-149. (8a-b) *Carcharhinus limbatus*, upper tooth, Algodão, MNUFRJ-ZA-05. (9a-b) *Carcharhinus plumbeus*, upper tooth, Algodão, MNUFRJ-ZA-44. (10a-b) *Galeocerdo cuvier*, tooth, Algodão, MNUFRJ-ZA-17. (11a-b) *Negaprion brevirostris*, upper tooth, Algodão, MNUFRJ-ZA-25. (12a-b) *Rhizoprionodon lalandii*, lower tooth, Bigode, MNUFRJ-ZA-87, and (13a-b) upper tooth, Algodão, MNUFRJ-ZA-70. (14a-b) *Rhizoprionodon porosus*, upper tooth, Bigode, MNUFRJ-ZA-88. (15a-b) *Sphyrna mokarran*, upper tooth, Caieira II, MNUFRJ-ZA-99. (16a-b) *Sphyrna zygaena*, lower tooth, Major, MNUFRJ-ZA-161. Scale bar: 1 cm. Views: labial (1b, 2a-5a, 6b, 7a, 8-10b, 11-13a, 14-15b, and 16a), lingual (1a, 2-5b, 6a, 7b, 8-10a, 11-13b, 14-15a, and 16b).

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counterpart. *Sphyrna* spp. size is nine times smaller than the common length estimation of the living counterpart and could be represented here by neonate specimens [in comparison with the adults body size (i.e., 370 cm TL [88])]. *Sphyrna* species are currently classified as an endangered species [105]. The size of *Carcharodon carcharias* is three times smaller than the common body length of their living counterpart (i.e., 541 cm TL for males and 594 cm for females

Fig 9. Ray teeth, vertebrae and dermal denticle from Rio de Janeiro shellmounds. (1a-b) *Pristis* sp., vertebrae, Usiminas, MNUFRJ-ZA-597 and, (2a-b) Algodão, MNUFRJ-ZA-624. (3a-c) *Rhinoptera* sp., tooth, Algodão, MNUFRJ-ZA-498, and (4a-c) Acaiá, MNUFRJ-ZA-708. (5a-b) Ray indet., vertebrae, Saquarema, MNUFRJ-ZA-Col.L.Kneip-08125. (6a-b) *Dasyatis centroura*, caudal spine, Saquarema, MNUFRJ-ZA-Col.L.Kneip-087-1. (7a-b) *Actobatus narinari*, lower plate fragment, Usiminas, MNUFRJ-ZA-424. (8–10) Dasyatidae indet., dermal denticle, Usiminas, MNUFRJ-ZA-407. Scale bar: 1 cm.

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[88]), which is classified as a vulnerable species [106]. The presence of small vertebrae (and some teeth) is suggestive of neonates of Lamnidae, Carcharhinidae, Sphyrnidae and Pristidae species and provides irrefutable support for the presence of pregnant females and juveniles in these nursery areas.

There are three criteria to identify an area as a nursery [107]: **(1)**, an area with a high frequency of sharks; **(2)**, an area to which shark species have a tendency to remain or return for extended periods; **(3)**, an area or habitat that is repeatedly used across years. Sharks' philopatry [108] and the evidence of residence and the site fidelity suggest that oceanic species preferentially return to their exact birthplaces (i.e., natal philopatry) or birth regions (i.e., regional philopatry) for either parturition or mating even though they make long distance movements that would allow them to breed elsewhere [109]. Modern philopatric are represented by Holocene species in the Brazilian shellmounds, and include *Carcharias taurus*, *Carcharodon carcharias*, *Carcharhinus leucas*, *C. limbatus*, *Galeocerdo cuvier* and *Negaprion brevirostris* [109].

Special remarks are made regarding the presence of cosmopolitan sharks with long-distance oceanic migration, such as *G. cuvier* and *C. carcharias*. The tiger shark, *G. cuvier*, spends the majority of its time in the upper 50 m of water and is recorded to migrate approximately 1,100 to 1,800 km [110,111,112]. The white shark, *C. carcharias*, during its 'patrolling' behavior, mostly swam in depths between 5 and 50 m and during migration, swam almost exclusively at the surface [113]. The long distance oceanic migration of this shark is record to be approximately 4,000 km between the Pacific coast of California and Mexico to the Hawaiian islands [113,114]. Both tiger and white sharks were represented in the shellmounds by perforated teeth, some of them recovered as pendant necklaces associated with human burials and bones [115]. Moreover, modern shark nursery areas were recognized in Brazil [116,117].

Fig 10. Shark and ray vertebrae from Rio de Janeiro shellmounds. (1a-c) *Carcharias taurus*, vertebrae, Usiminas, MNUFRJ-ZA-570. (2a-c) *Carcharodon carcharias*, vertebrae, Algodão, MNUFRJ-ZA-625, and (3a-b) Beirada, MNUFRJ-ZA-576. (4a-c) *Carcharias taurus*, vertebrae, Algodão, MNUFRJ-ZA-621. (5a-c) *Carcharhinus brevipinna*, anterior vertebrae, Usiminas, MNUFRJ-ZA-567, (6a-c) anterior vertebrae, Beirada, MNUFRJ-ZA-575, and (7a-c) posterior vertebrae, Usiminas, MNUFRJ-ZA-568. (8a-c) *Carcharhinus* sp., vertebrae, Usiminas, MNUFRJ-ZA-569. (9a-c) *Rhizoprionodon* sp., vertebrae, Usiminas, MNUFRJ-ZA-571. (10a-c) *Carcharhinus* sp., vertebrae, Algodão, MNUFRJ-ZA-620, (11a-c) Acaiá, MNUFRJ-ZA-715, and (12a-c) Algodão, MNUFRJ-ZA-623. (13a-c) *Sphyrna* sp., vertebrae, Usiminas, MNUFRJ-ZA-572, and (14a-c) Camboinhas, MNUFRJ-ZA-853. Scale bar: 1 cm.

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Estimated teleostean size class ranges in selected shellmounds, based on 5,532 otoliths of *Micropogonias furnieri*, showed a long history of fishery exploitation (ca 5,595 cal BP until today). The frequency distribution of whitemouth croaker, *M. furnieri*, body sizes based on otoliths from the Ponte do Girau, Algodão, Beirada, Manitiba and Camboinhas shellmounds, and the body size (TL) estimates from modern fisheries (i.e., artisanal and semi-industrial) in the Itaipu and Angra dos Reis regions, Rio de Janeiro State (Fig 4), suggest two modal

Fig 11. Teleostean otoliths from the Rio de Janeiro shellmounds. (1) *Albula nemoptera*, Algodão, MNUFRJ-ZA-190. (2a-c) *Bagre marinus*, Algodão, MNUFRJ-ZA-196. (3a-c) *Genidens genidens*, Camboinhas, MNUFRJ-ZA-845. (4) *Hemiramphus* sp., Caieira II, MNUFRJ-ZA-316, and (5) Caieira II, MNUFRJ-ZA-317. (6) *Centropomus ensiferus*, Algodão, MNUFRJ-ZA-206. (7) *Centropomus undecimalis*, Algodão, MNUFRJ-ZA-205. (8) *Epinephelus* sp., Major, MNUFRJ-ZA-269. (9) *Epinephelus marginatus*, Usiminas, MNUFRJ-ZA-521. (10) *Lutjanus synagris*, Algodão, MNUFRJ-ZA-228. (11) *Lutjanus* sp., Major, MNUFRJ-ZA-279. (12) *Ocyurus chrysurus*, Usiminas, MNUFRJ-ZA-519. (13) *Diapterus rhombeus*, Caieira II, MNUFRJ-ZA-306.

(14) *Diplodus* sp., Algodão, MNUFRJ-ZA-215, and (15) Algodão, MNUFRJ-ZA-217. (16) *Gerres cinereus*, Algodão, MNUFRJ-ZA-223. (17) *Anisostremus virginicus*, Algodão, MNUFRJ-ZA-192. (18) *Haemulon aurolineatum*, Usiminas, MNUFRJ-ZA-517. (19) *Haemulon sciurus*, Algodão, MNUFRJ-ZA-184). (20) *Haemulon steindachneri*, Algodão, MNUFRJ-ZA-220. (21) *Archosargus rhomboidalis*, Algodão, MNUFRJ-ZA-194. (22) *Archosargus* sp., Algodão, MNUFRJ-ZA-193. (23) *Bairdiella ronchus*, Algodão, MNUFRJ-ZA-203. (24) *Cynoscion jamaicensis*, Acaiá, MNUFRJ-ZA-876. (25) *Cynoscion microlepidotus*, Algodão, MNUFRJ-ZA-213. (26) *Cynoscion acoupa*, Manitiba, MNUFRJ-ZA-559. (27) *Larimus breviceps*, Algodão, MNUFRJ-ZA-226. (28) *Micropogonias furnieri*, Algodão, MNUFRJ-ZA-232. (29) *Pareques acuminatus*, Manitiba, MNUFRJ-ZA-875.

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distributions of body size frequencies, with overlap between prehistoric and modern fisheries. In comparison to the size estimated based on otoliths of *M. furnieri* from the shellmounds, a probabilistic tendency of a reduction in body size of 28% in modern catches may be attributed to overexploitation.

Despite *M. furnieri* being a species with medium resilience to fishing pressure (i.e., criteria based on values of selected life-history parameters: high fertility and high body growth parameter, K [118]), the regional assessments of current stocks indicate overexploitation [89,90]. Results indicate that body size medians between shellmounds and related environment/coastal geomorphology were significantly different (Fig 5). These differences could be interpreted as a consequence of seasonal variations of fishery areas and the intrinsic life history of the species.

The prehistoric fisheries and time series records along archaeostratigraphic sections vary from a single to seven layers based on the chronological sequences of settlements studied here, while the calibrated radiocarbon models, based on fish otoliths and shell samples by layer, show close or overlapping age probability distributions of individual shellmounds [52,53,55]. Consequently, the shallow profile of individual shellmounds studied here from Rio de Janeiro State could be treated arbitrarily as a single unit for the purpose of a fisheries analysis.

The results, in terms of richness, point toward an early stage of overexploitation of medium- to large-sized, vulnerable fish species, characterized by late maturity, slow growth, low reproductive rates, longevity, spawning aggregations and often ovoviviparous and/or viviparous life histories [119,120,121]. Groupers also exhibit slow growth, low reproductive rates and increased longevity, and reproductive adults leave shallow water habitats and move to deep waters after spawning [122,123]. Our results suggest that prehistoric fishing pressure on coastal areas was sufficient to cause the initial phase of population declines [58,124,125].

Prehistoric fishery methods were able to catch medium to large sharks, skipjack tunas, sailfish and groupers and could have included seined or floating gillnets, spears and long-lines. However, more resilient demersal species did not decline as drastically. Therefore, it is plausible that seasonal fisheries that used beach seines during high upwelling productivity contributed to massive catches of groundfish schools. Other small species could be caught by hooks or traps.

Sawfishes were present during prehistoric times in southeastern Brazil [126]; however, nowadays, these species are a nearly extinct taxon [127], and the last record of the great white shark was in the mid 80's [128]. *Carcharias taurus* is a common shark caught in summer in small numbers in artisanal gillnet fisheries on the Rio de Janeiro coast [128]. Nothing is known about the porbeagle shark, *Lamna nasus*, in the Brazilian region, a rare shark caught in longlines from the 60's to the 90's [129]. This species is distributed from southern Brazil and Uruguay to Argentina [130].

Diverse evidence of archaeological artifacts of gorges, bones and shell fishhooks (including an early fishhook, dated to 42,000 yr BP [131]) and fishing lines (from native fiber plants or human hair) used for inshore or pelagic fisheries was recorded worldwide [15,132,133]. The presence of projectile points in archaeological sites in California, USA (~ 12,200 to 11,200 yr BP) associated with marine and aquatic faunal remains is common [134]. Moreover, the only

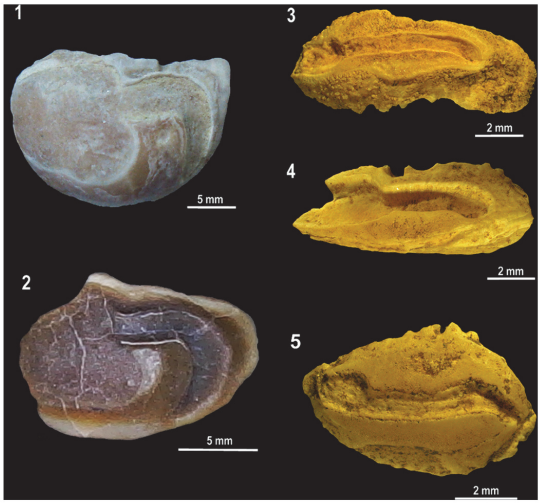

Fig 12. Teleostean otoliths from the Rio de Janeiro shellmounds. (1) *Pogonias cromis*, Ponte do Girau, MNUFRJ-ZA-562. (2) *Umbrina coroides*, Ilha do Cabo Frio, MNUFRJ-ZA-874. (3) *Mugil liza*, Algodão, MNUFRJ-ZA-233. (4) *Sphyraena guachancho*, Algodão, MNUFRJ-ZA-236. (5) *Hyporhamphus unifasciatus*, Algodão, MNUFRJ-ZA-2230.

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known evidence of fishery tools from Brazilian archaeological sites are manufactured bony spear-tips [30], without clear evidence of possible techniques for massive catches or refined manufacture of hooks used for pelagic or large demersal fishes (S4 Appendix).

Shark teeth are culturally significant in the worldview of indigenous mythology, and numerous archaeological burials of human skeletons in Brazilian shellmounds were decorated with necklaces made with drilled shark teeth [115]. Drilled shark teeth are also present in Argentinian and Uruguayan middens [135]. Individually, drilled shark teeth are here represented by *Carcharodon carcharias*, *Galeocerdo cuvier*, *Carcharhinus altimus*, *C. leucas*, *C. plumbeus* and *Sphyrna mokarran* (Fig 7). However, another possibility is the use of shark teeth for tool manufacturing, e.g., affixed to pieces of wood with vegetal fibers, similar to Polynesian artifacts [127], or as points of arrows.

The analysis of the ichthyofauna shows significant differences between expected fish assemblages (i.e., based on modern occurrences in the coastal area) and the record of observed species in shellmounds (Table 2, Figs 7–15). A high diversity of fish species in the shellmounds reveals the fishery and coastal navigation skills of ancient fishermen and the high importance of coastal fisheries for those prehistoric communities. Such prehistoric fishery activities on vulnerable species and special nursery areas could correspond to the beginning of fish stock depletion along the southeastern Brazilian coast. Overexploitation of such coastal fisheries became unequivocally intense during colonial times resulting in the near collapse of natural fish populations, especially affecting large-sized species such as sharks and giant groupers.

However, in terms of natural resources, we assume that eight biases might have affected the ichthyoarchaeological samples under study: **(1)**, selective targeting of certain species (i.e., unpalatable taste, poisonous fishes, small sizes, etc.); **(2)**, the inaccessibility of certain available species (e.g., limitations of employed fishing techniques or presence of adverse marine environmental conditions); **(3)**, minimal potential preservation of some species (i.e., some fishes such

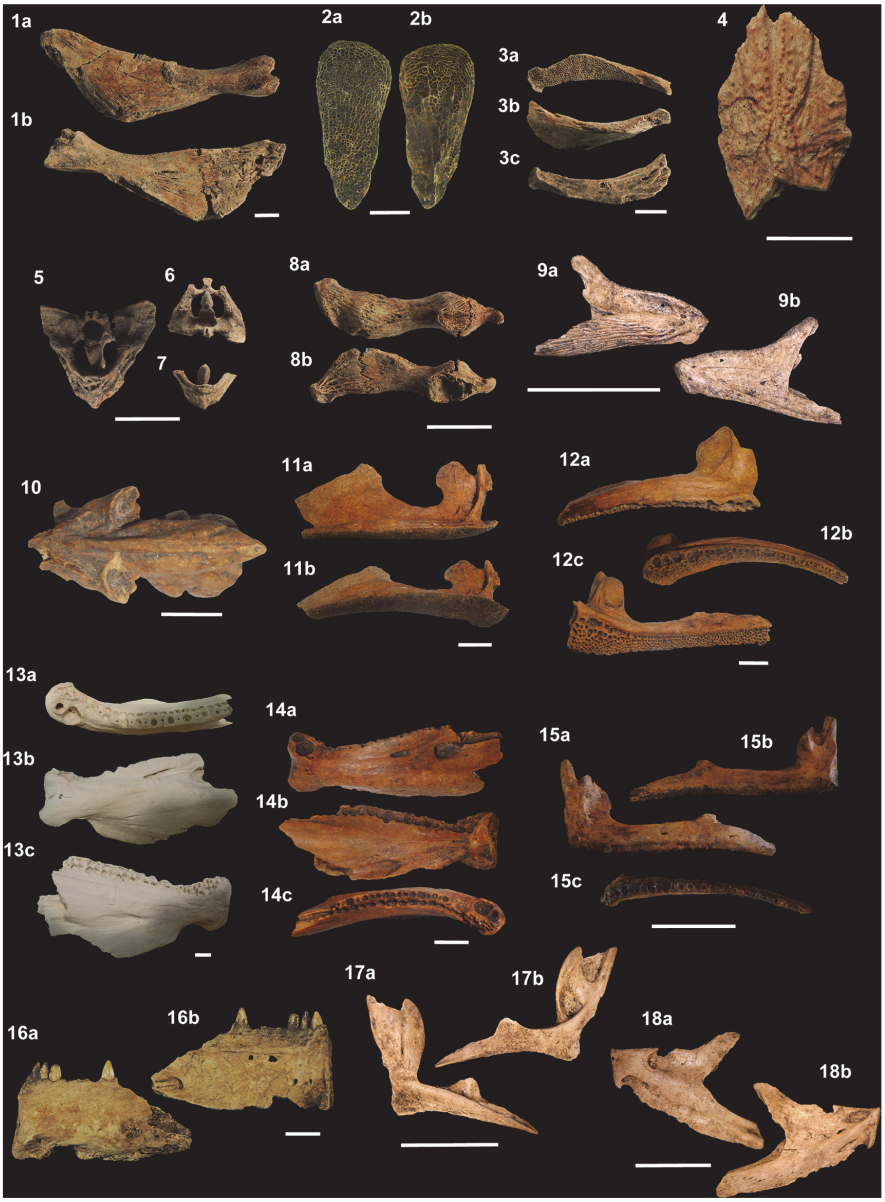

Fig 13. Teleostean skeletal remains from the Rio de Janeiro shellmounds. (1a-b) *Aspistor* sp., hyoid bar, Manitiba, MNUFRJ-ZA-537. (2a-b) *Bagre marinus*, frontal, Algodão, MNUFRJ-ZA-500. (3a-c) *Cathorops* sp., dentary, Manitiba, MNUFRJ-ZA-542. (4) *Genidens barbus*, supraoccipital, Manitiba, MNUFRJ-ZA-538. (5–7) *Genidens* sp., nucal plate, Manitiba, MNUFRJ-ZA-554, and (8a-b) hyoid bar, Manitiba, MNUFRJ-ZA-534. (9a-b) *Sargocentrum* sp., dentary, Acaiá, MNUFRJ-ZA-675. (10) *Centropomus parallelus*, supraoccipital, Usiminas, MNUFRJ-ZA-387. (11a-b) *Centropomus undecimalis*, premaxillary, Usiminas, MNUFRJ-ZA-439. (12a-c) *Epinephelus* sp., premaxillary, Usiminas, MNUFRJ-ZA-444, and (13a-c) dentary, Ilha do Cabo Frio, MNUFRJ-ZA-871. (14a-c) *Mycteroperca* sp., dentary, Usiminas, MNUFRJ-ZA-392. (15a-c) *Caranx* sp., premaxillary, Camboinhas, MNUFRJ-ZA-851, and (16a-b) dentary, Acaiá, MNUFRJ-ZA-744. (17a-b) *Selene vomer*, premaxillary, Acaiá, MNUFRJ-ZA-663, and (18a-b) dentary, Acaiá, MNUFRJ-ZA-667. Scale bar 1 cm.

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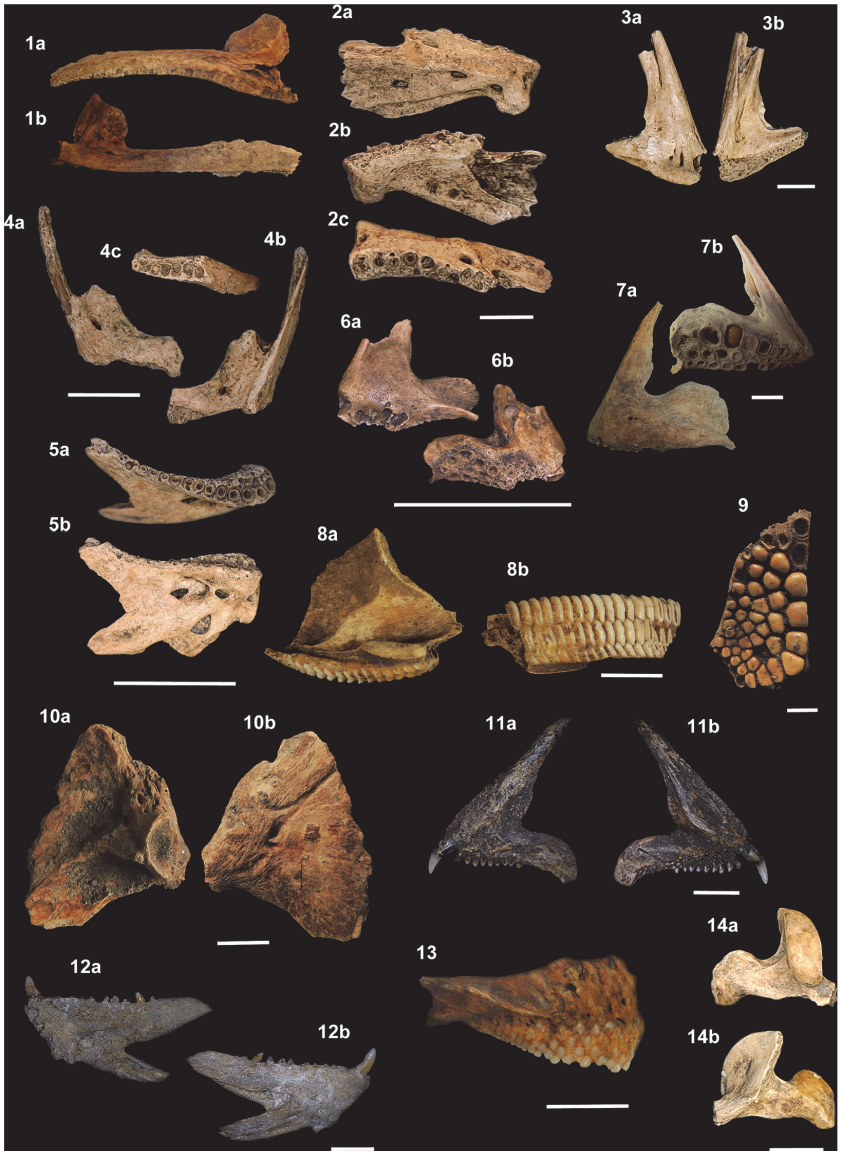

Fig 14. Teleostean skeletal remains from the Rio de Janeiro shellmounds. (1a-b) *Oligoplites saurus*, premaxillary, Usiminas, MNUFRJ-ZA-438. (2a-c) *Lutjanus* sp., dentary, Algodão, MNUFRJ-ZA-858. (3a-b) Gerreidae indet., premaxillary, Algodão, MNUFRJ-ZA-485. (4a-c) *Anisostremus* sp., premaxillary, Algodão, MNUFRJ-ZA-859, and (5a-b) dentary, Algodão, MNUFRJ-ZA-692. (6a-b) *Diplodus* sp., premaxillary, Acaiá, MNUFRJ-ZA-682. (7a-b) *Archosargus* sp., premaxillary, Ilha do Cabo Frio, MNUFRJ-ZA-873. (8a-b) *Sparisoma* sp., upper pharyngeal tooth plate, Acaiá, MNUFRJ-ZA-730. (9) *Pogonias cromis*, pharyngeal tooth, Manitiba, MNUFRJ-ZA-552. (10a-b) *Mugil* sp., opercle, Manitiba, MNUFRJ-ZA-550. (11a-b) *Bodianus rufus*, premaxillary, Acaiá, MNUFRJ-ZA-828, and (12a-b) dentary, Ilha do Cabo Frio, MNUFRJ-ZA-872. (13) *Sparisoma* sp., premaxillary, Usiminas, MNUFRJ-ZA-436. (14a-b) *Scarus* sp., maxillary, Algodão, MNUFRJ-ZA-993. Scale bar 1 cm.

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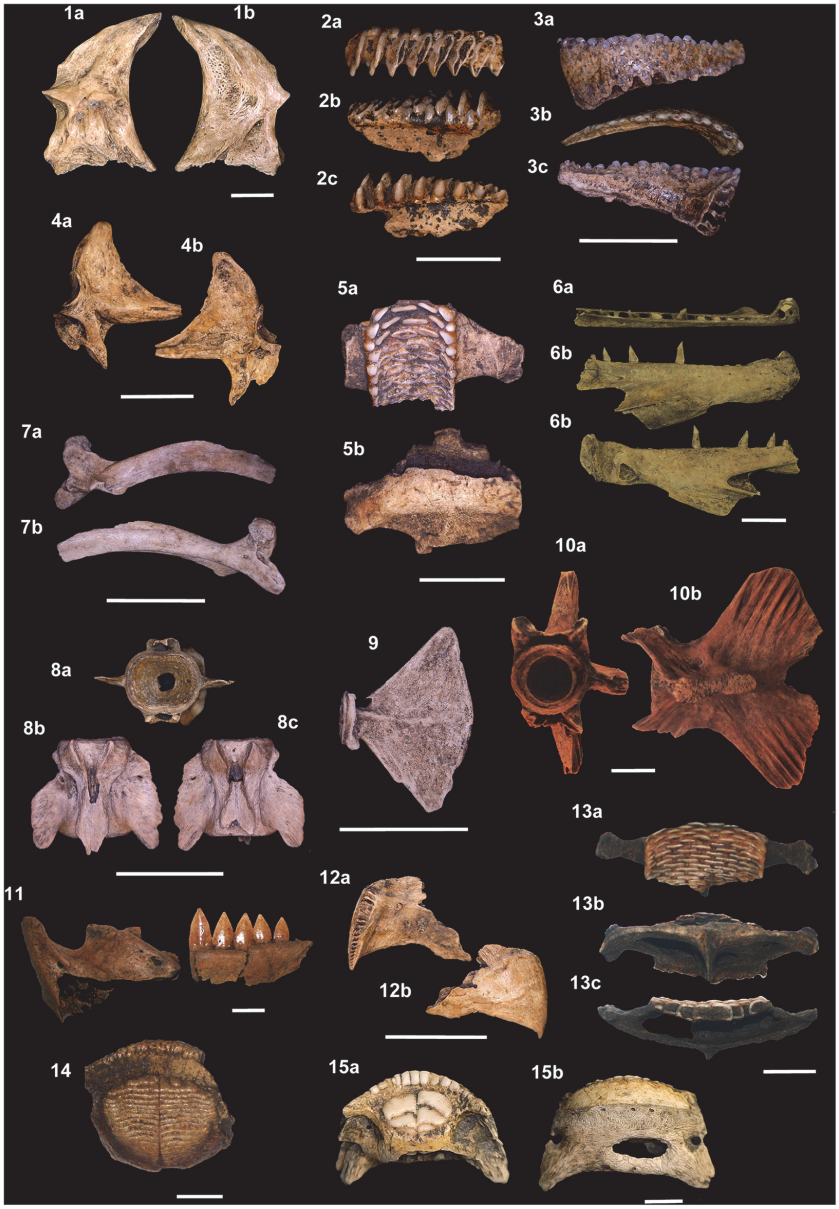

Fig 15. Teleostean skeletal remains from the Rio de Janeiro shellmounds. (1a-b) *Scarus* sp., angulo-articular, Algodão, MNUFRJ-ZA-496, and (2a-c) pharyngeal tooth, Acaiá, MNUFRJ-ZA-724. (3a-c) *Sparisoma* sp., dentary, Acaiá, MNUFRJ-ZA-720, and (4a-b) angulo-articular, Acaiá, MNUFRJ-ZA-666. (5a-b) *Scarus* sp., lower pharyngeal tooth plate, Acaiá, MNUFRJ-ZA-674. (6a-c) *Trichiurus lepturus*, dentary, Acaiá, MNUFRJ-ZA-746. (7a-b) *Katsuwonus pelamis*, maxillary, Acaiá, MNUFRJ-ZA-705, and (8a-c) vertebrae, Acaiá, MNUFRJ-ZA-710. (9) *Scomberomus* sp., hypural complex, Acaiá, MNUFRJ-ZA-701. (10a-b) *Istiophorus albicans*, hypural,

Usiminas, MNUFRJ-ZA-471. (11) *Sphyraena barracuda*, dentary, Usiminas, MNUFRJ-ZA-395. (12a-b) *Lagocephalus laevigatus*, premaxillary, Acaiá, MNUFRJ-ZA-679. (13a-c) *Sparisoma* sp., lower pharyngeal tooth plate, Usiminas, MNUFRJ-ZA-428. (14) *Diodon* sp., tooth plate, Usiminas, MNUFRJ-ZA-429. (15a-b) *Chilomycterus spinosus*, dentary, Algodão, MNUFRJ-ZA-487. Scale bar 1 cm.

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as sardines could be consumed entirely); **(4)**, non-uniform employment of archaeological sieving techniques (i.e., the use of large mesh sizes and loss of small stingray teeth such as those of *Dasyatis*, *Gymnura*, or *Mobula* species and otoliths, like those of syngnathids, cynoglossids, achirids, atherinids, bleniids and gobiids); **(5)**, archaeological priority (i.e., ichthyoarchaeological remains such as bones, teeth and otoliths could be considered of secondary importance during field activities, except when they exhibit holes, cutting or intentional abrasion); **(6)**, early overexploitation and fish stock depletion (i.e., large and diverse shark species and rocky reef fish are well represented only in the Angra dos Reis shellmounds); **(7)**, the presence of non-diagnostic or broken bones or eroded otoliths (i.e., unclassified species); and **(8)**, missing specimens.

Conclusions

Prehistoric fishery activity along the Rio de Janeiro coast under the influence of coastal marine upwellings was characterized by massive catches of demersal finfish that inhabit sandy and coastal marine lagoons (e.g., *Micropogonias furnieri*), rocky reef fishes caught near islands and islets (e.g., *Epinephelus morio*), and pelagic fishes caught near rocky cliffs and islands (e.g., *Istiophorus albicans*). Shark fisheries could have been located in nursery areas of protected rocky cliff bays in Arraial do Cabo, Cabo Frio Island, Angra dos Reis and Ilha Grande.

Prehistoric records of high elasmobranch diversity in the Ribeira Bay provide clear evidence for the exploitation of natural populations of sharks and rays since pre-colonial times, especially of bigger species such as the porbeagle shark, *Lamna nasus*, the sand tiger shark, *Carcharias taurus*, the great white shark, *Carcharodon carcharias*, and sawfishes, *Pristis* sp. All these are vulnerable species that could have been rare, especially when taking into consideration that today they are rare or present in reduced numbers in the Ribeira Bay or in the adjacent Angra dos Reis region.

Hence, the results produced here should be addressed as a baseline reference of the ichthyodiversity during the prehistoric times, promoting further debate on the relationships established with past fishing activities, as well as changes in local and regional oceanographic systems.

Supporting Information

S1 Appendix. Distribution of shellmounds along the South American coast.
(DOCX)

S2 Appendix. Ichthyoarchaeological material. Ichthyological collection, Zooarchaeology, Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ)–curators: Maria Cristina Tenório, Tânia Lima.
(DOCX)

S3 Appendix. Modern material. A. Ichthyological collection, Departamento de Biologia Animal e Vegetal—Instituto de Biologia, Universidade do Estado do Rio de Janeiro (UERJ)—curators: Ulisses Leite Gomes, Maisa da Cruz Lima, Cristina Paragó, Alexandra Pinto Quintans. B. Ichthyological collection, Otoliths, Departamento de Biologia Marinha—Instituto de Biologia,

Universidade Federal Fluminense (UFF)–curator: Orangel Aguilera. C. Ichthyological collection, Dry skeletons, Departamento de Biologia Marinha—Instituto de Biologia, Universidade Federal Fluminense (UFF)–curators: Orangel Aguilera.
(DOC)

S4 Appendix. The unknown prehistoric fishing. Artwork by Eduardo Agelvis.
(DOCX)

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Author Contributions

Conceived and designed the experiments: MSL TCPB RAT CMN OA. Performed the experiments: MSL TCPB RAT CMN ARGT JDCB MH KM OA. Analyzed the data: MSL TCPB RAT CMN ARGT JDCB MH KM OA. Contributed reagents/materials/analysis tools: LR MCT TL RS MH KM CC OA. Wrote the paper: MSL TCPB OAS. Revised and edited the manuscript: MSL TCPB RAT CMN ARGT JDCB TL OA.

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